THE EFFECTS OF MYCORRHIZAL TREATMENTS AND NITROGEN-PHOSPHORUS FERTILIZATION ON FIELD GROWTH OF SLASH PINE SEEDLINGS

By

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TO MY FATHER AND MOTHER

WHOSE CONSTANT INSPIRATIONS MADE THESE ALL POSSIBLE

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TABLE OF CONTENTS

ACKNOWLEDGMENTS iii

LIST OF TABLES viii

LIST OF FIGURES xii

ABSTRACT xv

INTRODUCTION 1

LITERATURE REVIEW 3

- Mycorrhizal Terminology 3
- Fungi Forming Ectomycorrhizae 4
- Carbon Nutrition of Mycorrhizal Fungi 4
- Significance of Mycorrhizal Associations 5
  - Afforestation and Reforestation Work 5
  - Role of Mycorrhizae in the Mineral Nutrition of Pine 6
    - Phosphorus 6
    - Other Nutrients 7
  - Role of Mycorrhizae in the Control of Soil-borne Plant Pathogens 7
- Conditions and Theories for the Formation of Ectomycorrhizal Roots 8
  - The Humus and Mineral Salt Theory 8
  - Bjorkman's Carbohydrate Theory 8
  - The "M" Factor Theory in Ectomycorrhizal Formation 9
  - Role of Growth Hormones in Ectomycorrhizal Formation 10
- The Ectomycorrhizal Fungi *Thelephora terrestris* and *Pisolithus tinctorius* 11
- Slash Pine in Relation to the Flatwood Sites of Florida 12

Current Management Practices to Increase the Productivity of Slash Pine 13

Tree Improvement 13
Site Preparation 13
Control of Water Table 13
Studies on Fertilizer Applications 14

MATERIALS AND METHODS 18

Culture Preparation of Mycorrhizal Fungi 18
Preparation of Mass Inocula 18
Synthesis of Ectomycorrhizae on Slash Pine Seedlings 19
Selecting and Grading Seedlings for Field Experiments 21
Field Experiments 21

Experimental Design 21
Physical and Chemical Properties of the Soil 24
Studies of the Movement of Applied Nitrogen and Phosphorus in the Soil Profile 25
Rainfall Data 27
Harvesting and Measuring Growth Parameters 27
Tissue Analyses 27

Morphological Characterization of Mycorrhizal Roots and Reisolation Experiments 28

RESULTS 29

Movement of Applied Nitrogen and Phosphorus in the Soil Profile 29
Rainfall Measurements 33
Seedling Parameters Prior to Outplanting 33
Survival of Seedlings in the Field 33
General Growth Responses of Field Grown Seedlings 39
Specific Growth Responses of Field Grown Seedlings 50

Height 50
Fresh Weight of Shoots 50
Oven-dry Weight of Shoots 61
Number of Secondary Branches 63
Length of Longest Secondary Branch 66
Stem Diameter 69
Length of Primary Root 71
Fresh Weight of Roots 77
Oven-dry Weight of Roots 77
Number of Secondary Roots 81
Length of Longest Secondary Root 81
Percent Mycorrhizae 84
Total Fresh Biomass 84
Total Dry Biomass 88

Tissue Analyses 92

  Nitrogen 92
  Phosphorus 92
  Potassium, Calcium, and Magnesium 96
  Aluminum and Iron 98
  Sodium and Copper 98
  Manganese and Zinc 99

Morphological Characterization of Ectomycorrhizal Roots and Reisolation Studies 99

DISCUSSION 124

SUMMARY AND CONCLUSIONS 139

BIBLIOGRAPHY 142

APPENDIX 151

BIOGRAPHICAL SKETCH 169

LIST OF TABLES

1. Physical and chemical properties of the top 0-15 cm layer of the soil prior to planting 26

2. Initial and final concentrations of total N, total P, and extractable P in the 0-15 cm layer of a Myakka (fs) soil fertilized with factorial combinations of 0, 22, and 90 kg N and P/ha 30

3. Initial and final total N, total P, and extractable P concentrations in the spodic horizon of a Myakka (fs) soil under unfertilized plots or plots receiving 90 kg N or P/ha 32

4. Monthly rainfall over the Austin Cary Forest during the experimental period 34

5. Initial growth parameters and mineral root and shoot concentrations of slash pine seedlings receiving the four mycorrhizal treatments 35

6. Survival of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 38

7. Analyses of variances (mean squares) of sh-ot parameters of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 51

8. Heights of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 52

9. Effects of N and P rates and corresponding regression equation on different shoot parameters of field-grown slash pine seedlings 53

10. Fresh weight of shoots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 55

11. Interactions between mycorrhizal treatments and P rates on various response parameters of field-grown slash pine seedlings 57

12. Interactions between mycorrhizal treatments and P rates on various response parameters of field-grown slash pine seedlings with corresponding regression equations 59

13. Oven-dry weights of shoots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 62

14. Number of secondary branches formed on field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 64

15. Interactions between mycorrhizal treatments and N rates on the responses of secondary branches of field-grown slash pine seedlings 65

16. Interactions between mycorrhizal treatments and N rates on various response parameters of field-grown slash pine seedlings with corresponding regression equations 67

17. Length of the longest secondary branch of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 68

18. Stem diameters of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer treatments 70

19. Number of stem flushes of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 72

20. Analyses of variances (Mean Squares) of root parameters of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 73

21. Lengths of primary roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 74

22. Effects of N and P rates and corresponding regression equations on root parameters of field-grown slash pine seedlings 75

23. Interactions between N and P rates on length of primary root of field-grown slash pine seedlings 78

24. Fresh weights of roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 79

25. Oven-dry weights of roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 80

26. Number of secondary roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 82

27. Length of longest secondary roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 83

28. Percent mycorrhizal roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 85

29. Analyses of variances (Mean Squares) of total fresh and oven-dry weights of field-grown slash pine seedlings receiving four mycorrhizal treatments and nine N-P fertilizer rates 86

30. Total fresh weights of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 87

31. Effects of N and P rates and corresponding regression equation on total fresh and oven-dry weights of field-grown slash pine seedlings 89

32. Total dry weights of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates.................................... 91

33. Nitrogen concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 93

34. Total N accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 94

35. Phosphorus concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 95

36. Total P accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates 97

37. Isolation of possible ectomycorrhizal fungi from different morphological forms of ectomycorrhizal roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments 115

LIST OF FIGURES

1. Block layout of a split-plot design with four mycorrhizal treatments as main plots and nine N-P fertilizer rates as sub-plots 23

2. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_0P_0 fertilizer rate 40

3. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_0P_1 fertilizer rate 41

4. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_0P_2 fertilizer rate 42

5. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_1P_0 fertilizer rate 43

6. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_1P_1 fertilizer rate 44

7. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_1P_2 fertilizer rate 45

8. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_2P_0 fertilizer rate 47

9. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_2P_1 fertilizer rate 48

10. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_2P_2 fertilizer rate 49

11. Form A ectomycorrhizae with simple dichotomous roots and brown fungal mantle (90 X). 100

12. Form B ectomycorrhizae with simple dichotomous roots, brown fungal mantle, and typical beaded appearance. Arrow indicate constrictions on the mycorrhizal roots. (90 X) 102

13. Form C ectomycorrhizae with simple dichotomous roots, black basal roots, and light brown fungal mantle (90 X) 103

14. Form D ectomycorrhizae with dichotomous or coralloid branches, a distinctive black fungal mantle, and typical clavate-shaped terminal roots (90 X) 104

15. Form E ectomycorrhizae with dichotomous or coralloid roots and black fungal mantle. Arrows indicate constrictions on the roots giving a beaded appearance (90 X) 105

16. Form F ectomycorrhizae with typically sessiled roots and white fungal mantle. (90 X) 106

17. Form G ectomycorrhizae which are sessile, with white fungal mantle, and longer mycorrhizal roots 107

18. Form H ectomycorrhizae which are sessile and with yellow-orange fungal mantle. (90 X) 108

19. Form I ectomycorrhizae which are supported on stalks (arrow), and fungal mantle appearing white, yellow, or brown. (90 X) 110

20. Form J ectomycorrhizae with compound-coralloid roots and brown fungal mantle 111

21. Form K ectomycorrhizae with compound-coralloid roots, black basal roots, and brown terminal roots 112

22. Form L ectomycorrhizae with compound-coralloid roots, grayish-purple basal roots, and whitish brown terminal roots. (90 X) 113

23. Form M ectomycorrhizae with densely coralloid branches, forming clumps of roots, and with brown fungal mantle. (90 X) 114

24. Microscopic characteristics of mycelia of isolate 1 showing clamp connections. (Edentified as Thelephora terrestris). 1,200 X 116

25. Microscopic characteristics of mycelia of isolate 2 showing clamp connections. (Identified as Pisolithus tinctorius) 1,200 X 118

26. Microscopic characteristics of mycelia of isolate 3. (Identified as Cenococcum graniforme strain 1) 119

27. Microscopic characteristics of mycelia of isolate 4. (Identified as Cenococcum graniforme strain 2 120

28. Microscopic characteristics of mycelia of isolate 5 with the presence of occassional clamp connections. (Identified as Laccaria laccata) 1,200 X 121

29. Microscopic characteristics of mycelia of isolate 6. (Unidentified). 1,200 X 123

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THE EFFECTS OF MYCORRHIZAL TREATMENTS AND NITROGEN-PHOSPHORUS FERTILIZATION ON FIELD GROWTH OF SLASH PINE SEEDLINGS

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Slash pine seedlings received four initial mycorrhizal treatments and were outplanted in a flatwood soil belonging to the Myakka series in Florida. The four mycorrhizal treatments consisted of seedlings inoculated with Thelephora terrestris (TT) or Pisolithus tinctorius (PT), seedlings which were uninoculated (UI), and seedlings which were grown under standard nursery conditions (SN). After four months of growth in the field, nine N-P fertilizer rates were applied to each mycorrhizal treatment. The fertilizer rates consisted of factorial combinations of 0, 22, and 90 kg N and P/ha. After 10 months, the seedlings were harvested and growth response parameters were measured. Mycorrhizal treatments and fertilization with N or P induced significant responses in height growth, fresh and oven-dry weight of roots and shoots, secondary branch formation, length of secondary branches and roots, stem diameter, frequency of stem flushes, length of primary root, ectomycorrhizal root formation, and total fresh and dry biomass production. The positive growth responses resulting from mycorrhizal treatments were in the order of: SN $\geq$ TT $\geq$ PT $\geq$ UI treatments.

Nitrogen rates affected the growth responses in the order of: $90 \geq 22 \geq 0$ kg N/ha. The degree of responses from P rates were: $90 = 22 \geq 0$ kg P/ha. Regression equations of the responses of seedlings to N and P rates were linear and quadratic, respectively.

Interaction between mycorrhizal treatments and N rates induced significant responses in number and length of secondary branches. Seedlings receiving the TT and PT mycorrhizal treatments and fertilized 90 kg N/ha produced more and longer secondary branches than other mycorrhizal-N treatments.

Interaction between mycorrhizal treatments and P rates occurred for fresh and oven-dry weights of shoots, and total fresh and dry biomass production. The SN and TT mycorrhizal treatments in combination with 90 kg P/ha produced significantly larger weight responses than did the other mycorrhizal-P treatments.

Seedlings receiving the TT mycorrhizal treatments produced better field-growth responses than ded those treated with PT. The ectomycorrhizal fungus _T. terrestris_ is more suited, therefore, than _P. tinctorius_ to the acidic and poorly drained Myakka soils of Florida.

Mycorrhizal treatments and N-P fertilization increased the accumulation of N, P, K, Ca, Mg, Al, Fe, Na, Cu, Mn, and Zn by root and shoot tissues.

Reisolation studies showed that the continuity of mycorrhizal colonization by _T. terrestris_ was maintained in the field and that _P. tinctorius_ was replaced gradually by other ectomycorrhizal fungi. Roots of the uninoculated seedlings were colonized by _T. terrestris_, _Cenococcum graniforme_, and _Laccaria laccata_.

Classification of ectomycorrhizal roots into morphological forms may aid in identifying the mycorrhizal symbiont.

Nitrogen and P fertilizers were lost from the surface 15 cm of the Myakka soil. Nitrogen concentration of the soil was increased from 0.050% to 0.081% after the application of 90 kg N/ha. The N concentration was reduced to 0.050% after 10 months. Total and extractable P concentrations of the soil (61 and 2 ppm, respectively) were increased to 96 and 34.9 ppm, respectively after the application of 90 kg P/ha. After 10 months, total and extractable P were reduced to 73 and 8.0 ppm, respectively. The differences between final and initial P concentrations showed that P was partly retained in the surface 15 cm of the Myakka soil. Accumulation of N and P occurred in the spodic horizon.

INTRODUCTION

Mycorrhizae are beneficial for tree growth. This symbiotic plant-fungus association increases root surface area for greater water and nutrient absorption, increases longevity of the infected roots for extended root function, and imparts root protection from pathogenic microorganisms. Because of these inherent benefits, mycotrophic plants usually have higher survival and growth rates than nonmycotrophic plants.

Little work had been done on the practical applications of mycorrhizae in full-scale field operations. The main reason for this is the absence of a practical method of mass-inoculating plants with mycorrhizal fungi. At present, nursery grown pine seedlings depend on natural sources for fungal inocula. Complicating the inocula-source problem are the standard fumigation practices applied to control common pathogenic soil fungi, nematodes, and weeds; but which may also eliminate or reduce mycorrhizal fungi in the nursery soil.

Nutrients, particularly nitrogen and phosphorus, play an important role in mycorrhizal formation and plant growth. Increasing rates of nitrogen (particularly NO_3-N) usually reduce mycorrhizal formations. On the other hand, phosphorus generally promotes root growth and development, thereby increasing potential sites for mycorrhizal infection. Since fertilizers are added routinely in pine nurseries, their impact on mycorrhizal formation should be evaluated critically.

√

The ideal goal of a pine nursery is to produce seedlings adequately colonized with mycorrhizal fungi, and containing sufficient nutrients in their tissues to meet adverse site conditions and overcome the shock of transplanting. To achieve this goal, effective strains of mycorrhizal fungi ecologically adapted to specific areas could be inoculated onto slash pine seedlings under nursery conditions. Inoculation could be done by basidiospores or vegetative mycelia of the desired fungus. This procedure would insure adequate source of inocula for root colonization.

The objective of this experiment is to study the effects of mycorrhizal treatments and fertilization with different N-P fertilizer rates on the growth of slash pine seedlings under field conditions.

LITERATURE REVIEW

Mycorrhizal Terminology

The term "mycorrhiza" (plural -zae) was first used by Frank (1885) in reference to the structure formed by a fungus (Gr. mykes) and plant roots (Gr. rhiza). This fungus-root association is a form of parasitism whereby the fungal endophyte invades and parasitizes the root of the host plant. Unlike harmful parasites, the fungus does not damage or kill the host but instead provides many physical and physiological benefits to the latter.

Roots of the Pinaceae have been classified into long and short roots (Harley, 1948; Hatch and Doak, 1933). Long roots include the principal tap root and secondary roots which serve to expand the root system into the soil. These roots form permanent structures which increase in diameter due to secondary growth. The apical meristem is covered with a distinct root cap. The long roots give rise to numerous short or feeder roots which become mycorrhizal. The short roots are slow-growing, lack secondary growth, and are short-lived. Mycorrhizal formation usually increases the longevity of short roots while uninfected ones soon abort (Robertson, 1953). Sometimes, mycorrhizal short roots are converted to long roots and renew unrestricted growth (Wilcox, 1967).

Mycorrhizal roots are usually divided into three distinct groups based on morphological and anatomical characteristics: ecto-, endo-, and ectendomycorrhizae. This study deals only with ectomycorrhizae, and hence, the other two forms will not be elaborated.

In ectomycorrhizae, the colonized root is covered with a compact fungal mantle (sheath) which may isolate the root completely from the soil. Hyphal strands (rhizomorphs) usually radiate outward into the soil from the fungal mantle thus increasing the volume of soil exploited for water and nutrients by the mycorrhizal roots. The fungal hyphae also colonize the cortical tissues but only around the cortical cells. The hyphae do not penetrate through the cortical cells or the endodermal layer. Ectomycorrhizal roots are easily differentiated from noninfected ones due to hypertrophy of the cortical tissues of colonized roots. In pines, morphological forms of mycorrhizal roots are usually seen as simple dichotomously branched, coralloid, or tubercular roots.

Fungi Forming Ectomycorrhizae

Melin (1923, 1925), Modess (1941), and Norkrans (1950) showed that the endophytes forming ectomycorrhizae are higher Hymenomycetes and Gasteromycetes. Trappe (1962) compiled a list of mycorrhizal fungi. Some common genera reported are Amanita, Boletellus, Boletinus, Boletus, Clitocybe, Collybia, Laccaria, Lactarius, Rhizopogon, Russula, Scleroderma, Strobilomyces, Suillus, Tricholoma, and Thelephora. The species Cenococcum graniforme (Sow.) Fred. and Winge, an asexual stage of the Ascomycetes Elaphomyces (Trappe, 1971) is also a very common mycorrhizal fungus (Lihnell, 1942).

Carbon Nutrition of Mycorrhizal Fungi

Mycorrhizal fungi obtain their carbon and energy requirements from the host plant. Melin (1925) hypothesized that ectomycorrhizal fungi utilize simple sugars, particularly glucose, as their carbon source. How (1940) found that the symbiont Boletus elegans (Suillus grevillei

(Klotzsch) Sing.) preferred glucose for maximum growth in culture, although xylose, fructose, sucrose, and maltose also yielded good growth. Palmer and Hacskaylo (1970) studied the utilization of 39 soluble and 13 insoluble carbon sources by the ectomycorrhizal fungi *Amanita rubescens* (Pers. ex Fr.) S. F. Gray, *Cenococcum graniforme*, *Rhizopogon roseolus* (Corda) Hallos, *Russula emetica* (Schaeff. ex Fr.) Pers. ex Fr., *Suillus cothurnatus* Sing., and *Suillus punctipes* (Peck) Sing. D-glucose and D-mannose increased mycelial weights of all six fungi. *R. roseolus* grew on 22 carbon sources, *C. graniforme* on 17, *A. rubescens* on 15, *R. emetica* and *S. cothurnatus* on 14, and *S. punctipes* on 11. This study indicated that simple sugars like glucose and mannose were preferred, although the fungi also used other carbon sources.

Significances of Mycorrhizal Associations

Afforestation and Reforestation Work

Mycorrhizal associations are beneficial to the host. Afforestation attempts where mycorrhizal fungi were absent resulted in poor seedling growth and survival(Mikola, 1970). However, where the proper fungi were present, seedlings maintained vigorous growth (Hatch, 1936, 1937; Mikola, 1955, 1970).

Studies in Puerto Rico have demonstrated the need for mycorrhizal associations on pine (Hacskaylo and Vozzo, 1967; Vozzo and Hacskaylo, 1971). Since 1900, attempts to grow *Pinus attenuata* Lemm, *P. caribaea* Morelet, *P. pinaster* Ait, *P. radiata* D. Don, and *P. torreyana* Parry were made. Seeds of these pines germinated and grew for a short time, but seedlings died after 4 or 5 months. Phosphorus fertilization alleviated the chlorotic condition of the seedlings but the effect was only evident for a short time. However, Pinus caribaea seedlings, previously inoculated with Cenococcum graniforme, Corticium bicolor, Rhizopogon roseolus, and Suillus cothurnatus gave better growth and survival.

Role of Mycorrhizae in the Mineral Nutrition of Pines

The structure of ectomycorrhizae, with their thick fungal sheath,the Hartig net, the numerous hyphal strands radiating outward into the soil, and the increased surface area due to root hypertrophy, facilitates nutrient and probably water absorption. Hatch (1937) observed that mycorrhizal Pinus strobus L. seedlings absorbed 234% more phosphorus, 86% more nitrogen and 75% more potassium than nonmycorrhizal plants growing in the same substrate.

Phosphorus

The use of radioisotopes has confirmed that mycorrhizae aided in nutrient absorption. Bowen and Theodorou (1967), Harley and Brierley (1954, 1955), Harley and McCready (1950, 1952a, b), Harley et al., (1953, 1954, 1956, 1958), Kramer and Wilbur (1949), Mejstrik (1970), Melin and Nilsson (1950), and Morrison (1961a) showed that mycorrhizal roots readily absorbed ^{32}P from the external medium in greater proportions than nonmycorrhizal roots. Stone (1949), studying phosphorus nutrition of Pinus radiata concluded that one outstanding contribution by mycorrhizal fungi was the uptake of soil phosphorus normally unavailable to the plant.

Mycorrhizae of beech (Fagus sylvatica L.) were observed to absorb more phosphorus than nonmycorrhizal roots (Harley and McCready, 1950). Ninety percent of the accumulated phosphorus were in the fungal sheath (Harley and McCready, 1952a, b; Harley et al., 1953). Melin and Nilsson (1950) showed that ^{32}P absorbed by the hyphae of Boletus variegatus

(Suillus variegatus (Swartz ex Fr.) O. Kuntze) from external sources was later translocated to the root tissues of Pinus sylvestris L.

Other Nutrients

In addition to phosphorus, mycorrhizal fungi also increased the absorption of potassium (Harley and Wilson, 1959; Rosendahl, 1942), calcium (Melin and Nilsson, 1955), nitrogen (Carrodus, 1966; Doak, 1955; Melin and Nilsson, 1952, 1953; Lundeberg, 1970), and sodium (Melin et al., 1958).

Role of Mycorrhizae in the Control of Soil-borne Plant Pathogens

Mycorrhizae have been implicated as a biological deterrent to infection by root pathogenic fungi. Zak (1964) proposed that fungal symbionts can protect delicate, unsuberized root tissues from pathogenic fungi by utilizing surplus root carbohydrates, serving as a physical barrier to infection, secreting antibiotics, and favoring protective rhizosphere organisms. Marx (1967, 1969a, b, c), Marx and Davey (1969a, b) found mycorrhizae of Pinus echinata Mill and P. taeda L.seedlings resistant to infection by zoospores of Phytophthora cinnamomi Rands, the causal organism of littleleaf disease of these two pine species. Testing for antibiotic production, Marx (1967, 1969b) found that Leucopaxillus cerealis var. piceina (Peck) produced diatretyne nitrile, diatretyne amide, and diatretyne-3. Diatretyne nitrile inhibited the germination of zoospores of P. cinnamomi at 50 ppb and was lethal to zoospores at 2 ppm. Marx (1970) also found ectomycorrhizae formed aseptically on Pinus echinata seedlings by Thelephora terrestris (Ehrh.) Fr. and Pisolithus tinctorius (Pers.) Coker and Couch were resistant to infection by vegetative mycelia of P. cinnamomi. Both the fungal mantle and Hartig net of these ectomycorrhizae appeared to function as physical barriers to infection by the pathogen.

Conditions and Theories for the Formation of Ectomycorrhizal Roots

The Humus and Mineral Salt Theory

Several conditions and theories have been proposed to explain mycorrhizal formation. Frank (1885) observed a direct correlation between the abundance of mycorrhizae and the humus content of the soil. He then proposed the "humus theory" which suggested that mycorrhizae were organs concerned with the utilization of forest humus. Later, Stahl (1900) observed that mycorrhizal formation decreased with increasing soil fertility. He therefore postulated the "mineral salt theory" which stipulated that plants incapable of absorbing large amounts of salts because of restricted roots and limiting mineral nutrients, became mycotrophic. Hatch (1937) later proposed the "physical basis of mycotrophy" which in essence is similar to Stahl's theory. Hatch concluded that mycorrhizae were produced in abundance only when there is an imbanlance in the availability of one or more of the four elements: nitrogen, phosphorus, potassium, and calcium.

Bjorkman's Carbohydrate Theory

At the physiological level, Bjorkman (1940, 1942) proposed the "carbohydrate theory" which suggested that mycorrhizal formation is dependent on the presence of excess simple carbohydrates in the plant roots. Bjorkman demonstrated that mycorrhizae developed best in light exceeding 25% of full daylight and with a slight deficiency of easily available nitrogen or phosphorus. Bjorkman (1950) observed that there was a definite connection between carbohydrate production i.e., presence of excess soluble carbohydrates in roots and the formation of mycorrhizae. He also found that the effects of nitrogen and phosphorus were indirectly due to their influence on carbohydrate production and/or availability. High nitrogen fertility decreases the amount of excess carbohydrate, thus reducing mycorrhizae formation.

Bjorkman (1944) supported his theory by strangulation experiments with 3-year old Pinus sylvestris. Using thin wires, he restricted phloem translocation of sugar from the foliage to the roots. He found that strangulated plants had stunted roots and poor mycorrhizal development. Conversely, nonstrangulated plants had well developed mycorrhizal roots. Other workers (Harley and Waid, 1955; Wenger, 1955; Hacskaylo and Snow, 1959) showed strong relationship between light intensity and the amount of mycorrhizal development.

Several objections have been raised against Bjorkman's carbohydrate theory. Young (1947) showed that Boletus granulatus (Suillus granulatus (L. ex Fr.) O. Kuntze) can provide the roots of Pinus taeda with a carbohydrate supply derived from cellulose degradation even in a carbon dioxide-free atmosphere. Fortin (1966) synthesized mycorrhizae on excised roots of Pinus sylvestris by inoculation with Amanita rubescens on a carbohydrate-free medium.

The "M" Factor Theory in Ectomycorrhizal Formation

Melin (1954, 1962, 1963) studied the effects of root metabolites on tree mycorrhizal fungi using excised roots of Pinus sylvestris. He concluded that the pine roots exuded one or more growth promoting metabolites the "M" factor, which consisted of two components -- one diffusible through the plasma membrane, the other bound within the cells. Later, Melin (1963) suggested that cultured *Pinus sylvestris* roots contained, in addition to the M-factor and other growth promoting metabolites, one or more growth-inhibiting substances. Thus Melin's studies revealed that a complex of substances, M-factor plus inhibitors produced by the higher symbiont, were involved in the formation of tree mycorrhizae.

Role of Growth Hormones in Ectomycorrhizal Formation

Slankis (1951, 1957) working with excised *Pinus sylvestris* roots cultivated under aseptic conditions and inoculated with *Boletus luteus* (*Suillus luteus* (L. ex Fr.) S.F. Gray) and *B. variegatus* (*Suillus variegatus*) found that some substances exuded by the mycelia of the fungi induced short root swellings which resembled simple mycorrhizae. Slankis (1957) found that indoleacetic acid (IAA), indolebutyric acid, indolepropionic acid, and alphanaphthaleneacetic acid induced similar morphological structures. A close relationship was observed between the degree of deviation in root morphology and the concentration of auxin applied (Slankis, 1951, 1957). Forms resembling simple mycorrhizaw were produced by *Pinus strobus* roots using low concentrations (1-2 mg per liter) of IAA, coralloid branching was produced by medium concentrations (5-10 mg per liter), and tuberculate forms were produced at higher concentrations (10-20 mg per liter). If auxin was removed, root elongation was renewed. Slankis (1959, 1967) also observed a striking similarity between mycorrhiza-like structures induced by synthetic auxin and those induced by an unidentified fungal symbiont at low nitrogen concentration. Renewed growth of ectomycorrhizae by increased nitrogen concentrations was analogous to the renewed growth of synthetically induced mycorrhiza-like roots after auxin addition was discontinued.

Slankis (1971) concluded that the cessation of the symbiotic relationship suggests that the physiological state in mycorrhizal roots is one of the conditioning factors in the formation of the symbiotic relationship. To maintain the specific physiological state, the fungus must provide a continuous stream of auxin to the invaded rootlets. The auxin should be of a concentration which arrests the elongation of nonmycorrhizal roots and induces the characteristic mycorrhizal morphology. Since high nitrogen concentration caused termination of the symbiosis, Slankis (1959) hypothesized that the formation of the mycorrhizal structure *i.e.*, the establishment of a specific physiological state, was controlled by nitrogen through a fungus-auxin interaction.

The Ectomycorrhizal Fungi Thelephora terrestris and Pisolithus tinctorius

T. terrestris and *P. tinctorius* are two ectomycorrhizal fungi commonly isolated from slash pine seedlings (Marx and Bryan, 1970). Marx *et al*. (1970) observed that *T. terrestris* is a pioneer colonizer of fumigated soil. Marx and Ross (1970) reported that basidiospores of *T. terrestris* introduced into soil with aseptically grown *Pinus taeda* seedlings formed abundant ectomycorrhizae after 2½ months. Because of the prolific nature of basidiocarp formation by *T. terrestris*, basidiospores may be the main mechanism for inoculum dispersal of this fungus.

Currently, *P. tinctorius* has attracted major interest because of its high temperature tolerance and its presence on adverse forest sites. Using aseptic culture conditions, Marx *et al*. (1970) found that *P. tinctorius* formed more ectomycorrhizae on *Pinus taeda* seedlings as substrate temperature increased, as compared to *Thelephora terrestris*. Approximately 80% of the feeder roots were ectomycorrhizal by *P. tinctorius* at 34°C while *T. terrestris* did not form ectomycorrhizae at this temperature. These observations have received practical application when pine seedlings inoculated with P. tinctorius and outplanted on strip mining areas grew relatively well (Marx, personal communication). The strip mining areas are usually adverse sites due to high soil temperature, high soil content of toxic metals and with very high acidities.

Slash Pine in Relation to the Flatwood Sites of Florida

Slash pine (Pinus elliottii Engelm var. elliottii) is a host for several mycorrhizal fungi. Zak and Marx (1964) isolated fungal symbionts from ectomycorrhizae of 4 year old slash pine seedlings growing in openings within a 20 year old slash pine plantation in Georgia. They were able to isolate 22 different species groups based on cultural characteristics. Zak and Bryan (1963) isolated about 40 different fungal species from mycorrhizal roots of Pinus echinata, P. taeda, P. elliottii var, elliottii, and P. palustris Mill. These studies indicated that several fungi can form ectomycorrhizae with slash pine.

The north-central part of Florida is covered with second growth pine forests. Most of these areas include the flatwoods -- typically low, nearly level sands, supporting pine, palmetto, wire grass, and occassionally cypresses. These soils are not used extensively for agriculture due to high fluctuating water tables and low native fertility. Most of the soils are acidic and deficient in nitrogen and phosphorus. Other soils are deficient in potassium and certain micronutrients as well (Pritchett and Smith, 1970).

Slash pine is one of the most important pine species used for reforestation purposes in Florida. It adapts quite readily to the moist, infertile sands of the Lower Coastal Plains (Pritchett and Smith, 1970). Slash pine is important economically because it grows rapidly and yields more gums and high quality wood for pulping, posts, piles, and veneers.

Current Management Practices to Increase the Productivity of Slash Pine

To increase forest production, particularly in slash pine plantations new management practices involving tree improvement, site preparation, control of water table, insect and disease control, and soil fertilization are being explored.

Tree Improvement

Current tree improvement efforts are directed towards selecting pine progenies exhibiting better survival ability, height growth, fertilizer responses, and resistance to fusiform rust (Cooperative Forest Genetics Research Program Annual Report, 1971). Preliminary information shows that there is great potential in using tree improvement techniques to solve prevailing problems in growing pine plantations.

Site Preparation

Haines and Pritchett (1964, 1965), comparing bedded and unbedded sites, observed 68% and 100% increase in diameter and height growth, respectively, of slash pine in bedded sites. They observed that soil bedding increased root penetration and lateral root distribution.

Control of Water Table

White and Pritchett (1970) and White *et al*. (1971) studied the effect of fertilization and water control on height and biomass production of slash and loblolly pines on a Leon sandy soil. They observed that fine root biomass increased 145% by fertilization with 392 kg of diammonium phosphate alone. Water table control had no effect on fine root production. Total root biomass increased 58% by fertilization.

Maintaining the water table at 46 and 92 cm increased root biomass by 69 and 43%, respectively over that obtained from fluctuating water tables.

Studies on Fertilizer Applications

The first reported fertilization experiments in Florida (Pritchett and Swinford, 1961) involved single applications of 0.5 to 2 tons of colloidal phosphate per acre made at time of planting of slash pine. Significant increases in tree growth over a 15 year period were observed. In a different experiment, Curtis (1964) observed a 420% volume increase over control, 3 years after aerial fertilization of slash pine with 224 kg/ha of concentrated superphosphate.

Pritchett and Llewelyn (1966) studied growth response of slash pine to different rates of phosphorus from rock phosphate or superphosphate applied to sandy soils. They observed that rock phosphate or superphosphate band-applied to slash pine, 1 year after transplanting, resulted in significant height and diameter increases in 5 of 8 experiments, 3 to 5 years after applications. Responses occurred only on poorly drained (flatwood) sands. After the third year, 140 lb P/A from rock phosphate furnished results as good as 35 lb P/A of superphosphate. This study showed that greater initial height was obtained with superphosphate but eventually, rock phosphate proved to be more effective. Constructing growth curves on the same area, Pritchett (1969) observed an increase of the site indices from 8.5 m in control plots to 20.7 m in phosphorus treated plots in a wet savannah (Weston fsl). In deep sands, however, phosphorus treatments increased site indices by only a few feet.

Although growth stimulation by phosphorus was observed, growth retardation was obtained where nitrogen was applied, especially on phosphorus deficient sites. Maftoun and Pritchett (1970), applying 50 to 400 ppm nitrogen as $NaNO_3$ or $(NH_4)_2SO_4$, suppressed growth, total phosphorus uptake, and recovery of fertilizer phosphorus by young slash pine in two phosphorus deficient Coastal Plain soils. At the 200 and 400 ppm levels, growth was limited by $(NH_4)_2SO_4$ and all seedlings were killed at these rates by $NaNO_3$ in pot experiments. Root development was restricted by the nitrogen fertilizers to a greater extent than was top growth. Pritchett (1972), observing growth of slash and loblolly pines on Weston fsl soil in greenhouse studies indicated a reduction in early growth where nitrogen was applied. Mycorrhizal development was significantly reduced by nitrogen applications but was increased by phosphorus application (Pritchett, 1972). A ratio of nitrogen to phosphorus of less than 20:1 in the needles was needed for extensive mycorrhizal development.

Many theories have been suggested to explain the growth depressing effect of nitrogen. Bengtson and Jorgensen (1971) suggested that application of acid-forming nitrogen fertilizers reduced soil phosphorus availability as a consequence of increased iron and aluminum activity. They also suggested a direct suppression of mycorrhizae or root development following nitrogen fertilization, resulting in reduced phosphorus uptake. Pritchett and Smith (1967) proposed that high soluble salts around roots can hamper root development. Nitrogen also favors growth of weeds, resulting in competition with pine seedlings.

At present, most of the nitrogen fertilizers used are highly soluble and are easily leached from the root zone. Complicating the problem is the relatively low cation exchange capacity of most Florida soils. Bengtson and Voigt (1962), working with greenhouse lysimeters, observed that NH_4NO_3 applied to the surface of a Lakeland fine sand was leached from the upper 12 inches within four weeks when water was applied at the rate of 4 in/week. They also observed that the presence of 1 year old slash pine seedlings prevented or reduced the leaching of nitrogen at low and intermediate levels but not at high watering levels.

Because of the inherent leaching problem associated with use of soluble nitrogen sources, the application of slow-release nitrogen like ureaformaldehyde and sulfur-coated urea had been studied. Bengtson and Voigt (1962) observed lower leaching losses from ureaformaldehyde than from NH_4NO_3 in greenhouse lysimeter studies in Lakeland fine sand. Smith et al. (1971) observed that at low rates, soluble nitrogen sources appeared to be most effective. As rates were increased, height growth or diameter increment of slash pine seedlings diminished and mortality increased. The effect was pronounced when nitrogen fertilizers were applied at the time of transplanting. However, ureaforms did not show increase and/or severe damage even at the highest rates.

Despite the initial problem with nitrogen on phosphorus deficient sites, growth increases were obtained where phosphorus was added in factorial combinations with nitrogen. The Cooperative Research in Forest Fertilization (CRIFF) program installed uniform fertilizer experiments on 29 different sites in the Lower Coastal Plains. NH_4NO_3 was applied at rates of 0, 20, and 80 lb N/A in factorial combinations with three similar rates of phosphorus from concentrated superphosphate (CRIFF Progress Report, 1970-1971). The fertilizer were applied in 1.2 m band along rows of slash pine seedlings.

A significant height increase was obtained one year after application of nitrogen on 16 of the 29 sites. Increased heights were particularly significant at the flatwood sites (particularly where phosphorus was also added) where average height of trees treated with 0, 20 and 80 lbs N/A were 49.7, 54.3, and 60.9 cm respectively. Therefore, a synergistic effect of phosphorus on height growth was observed when it was applied in combination with levels of nitrogen fertilizers.

Slash pine is one economically important forest tree species in Florida. Present sites relegated to this species are the poorly drained, highly infertile soils. Slash pine, however, has responded positively to N-P fertilization in these sites. Because of the number of fungi capable of forming ectomycorrhizae with slash pine, and the concommitant importance of mycorrhizae _per se_, it is therefore important to study the feasibility of inoculating specific mycorrhizal fungi onto slash pine seedlings, imposing various levels of N-P fertilizers and observing the effects of the above treatments on pine growth. The following experiments investigated some of these problems.

MATERIALS AND METHODS

Culture Preparation of Mycorrhizal Fungi

Cultures of Thelephora terrestris (Ehrh) Fr.* and Pisolithus tinctorius (Pers.) Coker and Couch were grown in sterile 10-cm diameter Petri-dishes containing 30 ml modified Melin-Norkrans (MMN) agar medium (Marx, 1969). The medium contained: $CaCl_2$ 0.050 g, NaCl 0.025 g, KH_2PO_4 0.500 g, $(NH_4)_2HPO_4$ 0.250 g, $MgSO_4.7H_2O$ 0.150 g, malt extract 3.0 g, sucrose 10 g, agar (Difco) 15.0 g, thiamine HCl 100 µg, and $FeCl_3$ (1% solution) 1.2 ml in 1000 ml distilled water. The MMN medium was sterilized prior to use by autoclaving at 115°C for 15 minutes. The pH of the solution after autoclaving was 5.5. About 20 plates were prepared to initiate the mass inocula for each symbiont. The cultures were grown for 3 weeks in an incubator maintained at 25°C.

T. terrestris was isolated formerly from a shortleaf pine (Pinus echinata) ectomycorrhizae (Marx et al., 1970). P. tinctorius was isolated from a sporophore found in a pine plantation (Marx and Bryan, 1969). Both isolates formed ectomycorrhizae with slash pine seedlings in pure culture synthesis experiments (Marx and Bryan, 1970).

Preparation of Mass Inocula

Mass inocula of T. terrestris and P. tinctorius were grown in two 1

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* Cultures obtained from D. H. Marx, Principal Plant Pathologist, USDA Forest Service, Forestry Sciences Laboratory, Carlton Street, Athens, Georgia, 30601.

Mason jars. The cap of the jar permitted gaseous exchange between the interior of the jars and the atmosphere (de la Cruz, 1971). Laminated plastic sheets were cut into circles to perfectly fit the mouth of the jar. A hole (15 mm diameter) was bored through the center of the sheet and fitted with a 7.5 cm long glass tube. The glass tube was sealed with the plastic with GE silicone rubber RTV 60. The same sealant was used to glue the plastic sheet onto the cap. A cotton plug was inserted in each glass tube and the upper mouth of the tube was covered by a test-tube cap. Air exchange was obtained through the glass tube. The cotton plug and the test tube cap prevented aerial contamination.

A vermiculite-peat moss mixture was poured into each jar. The mixture contained approximately 970 cc vermiculite and 30 cc finely divided peat moss (Marx and Zak, 1965). The vermiculite was screened to remove the fine particles and only materials retained on a number 10 mesh was used. The peat moss was also screened to remove big organic debris. Five hundred ml MMN (without agar) was added to each jar and all jars were autoclaved for 20 minutes at 115°C.

Agar discs (1 cm diameter) were cut from the advancing front of pure cultures of *T. terrestris* or *P. tinctorius*.Five agar discs were placed in each jar. Certain jars were left noninoculated to serve as controls. The inocula were incubated for 4 months at 28°C.

Synthesis of Ectomycorrhizae on Slash Pine Seedlings

About 30 jars, each of *T. terrestris*, *P. tinctorius*, and noninoculated controls, were used for soil infestation. *T. terrestris* and *P. tinctorius* had completely permeated the vermiculite-peat moss substrate with mycelium. The mycelial clumps of *T. terrestris* or *P. tinctorius* were broken up by passage through a wire mesh. The inocula were then wrapped with cheesecloth and leached with distilled water to remove non-assimilated nutrients. The noninoculated vermiculite-peat moss mixture was processed identically.

Plastic containers (approximately 9x9x12 cm) with small drain holes were cleaned by soaking in hot water (80^{o}C) for 10 minutes. Synthesis of ectomycorrhizae on slash pine seedlings were done in a special electronically-air filtered growth room in Athens, Georgia (Marx, 1973). Approximately 120 cc of steam sterilized pebbles were placed in each plastic container. About 900 cc of a soil-inoculum mixture was then added into each pot. The mixture was done inside the growth chamber with the aid of a cement mixer at a ratio of 4:1 soil to inoculum. The soil was a mixture of a forest clay loam and sand (2:1 v/v) and had previously been steamed for 6 hours on three consecutive days.

Ninety containers were prepared for each of P. tinctorius, T. terrestris, and control treatment. Containers with T. terrestris were placed on a greenhouse bench outside the growth room for mycorrhizal synthesis. T. terrestris produces copious basidiocarps and the ensuing basidiospores would otherwise contaminate other seedlings in the growth rooms.

Approximately 10 aseptic slash pine seeds were sown in each container. The seeds were first washed in detergent solution for 5 minutes, soaked in 1% H_2O_2 solution for 48 hours at 5^{o}C, and then surface sterilized in 30 % H_2O_2 for 20 minutes. The seeds were then rinsed 10 times with sterile water to remove residual H_2O_2. After the seeds had germinated, the best 2 seedlings were selected from each pot while the others were clipped off. The seedlings were grown for 5 months. Seedlings were watered twice a week during the 5-month period. All seedlings were fertilized with 50 ml of the inorganic salts of MMN medium 1 month after seed germination.

Selecting and Grading Seedlings for Field Experiments

After the fifth month, all seedlings were lifted and graded to similar size and proper mycorrhizal condition (nonmycorrhizal for noninoculated seedlings. Seedlings grown in soil inoculated with *T. terrestris* or *P. tinctorius* were examined for the distinct ectomycorrhizae formed by the respective symbiont. *T. terrestris* forms ectomycorrhizae with a white fungal mantle, while *P. tinctorius* forms one with a yellow mantle. Inoculated seedlings, which were either too small, too large, or with poor mycorrhizal development were eliminated. Roots of noninoculated seedlings were examined to confirm absence of mycorrhizae.

Slash pine seedlings were also lifted from the Container Corporation Nursery, Archer, Florida. The seedlings were 8 months old at the time of lifting (3 months older than the Georgia-grown seedlings) and had mycorrhizal roots formed by naturally occurring fungal symbionts. These seedlings were graded in the same way as those grown in Georgia.

Five seedlings were randomly selected from each of the four seedling group and measured for height, root length, fresh and oven-dry weight of roots and shoots, number of lateral roots, percent mycorrhizal roots, and length of primary roots. The tissue was analyzed for N, P, K, Ca, Mg, Al, Fe, Na, Mn, Cu, and Zn. These measurements represent the initial size of the seedlings prior to outplanting.

Field Experiments

Experimental Design

A flatwood site was selected in the Austin Cary Memorial Forest, 19 km northeast of Gainesville, Florida. The site was prepared by roll chopping the native vegetation, discing the soil, and raking away the plant debris. Three blocks, each with a dimension of 32.90 x 43.87 m, were established. Within each block, four ectomycorrhizal treatments as main plots and nine N-P fertilizer rates as sub-plots were installed in a split-plot design. The four ectomycorrhizal treatments were seedlings with:

1.	*T. terrestris*	(TT)
2.	*P. tinctorius*	(PT)
3.	Uninoculated	(UI)
4.	Standard nursery-grown	(SN)

The nine fertilizer rates were as follows:

1.	N_0P_0	0 kg N/ha	0 kg P/ha
2.	N_0P_1	0	22
3.	N_0P_2	0	90
4.	N_1P_0	22	0
5.	N_1P_1	22	22
6.	N_1P_2	22	90
7.	N_2P_0	90	0
8.	N_2P_1	90	22
9.	N_2P_2	90	90

Each block had 36 different treatment plots representing different combinations of the four ectomycorrhizal treatments and nine N-P fertilizer rates. After the blocks and treatment plots were established, the seedlings were planted by hand. Each block was composed of nine rows spaced 1,83 m apart, each corresponding to one of the nine fertilizer rates (Figure 1). In all rows, groups of 5 seedlings from each of the

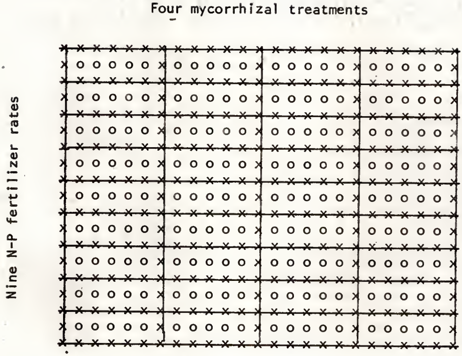

Figure 1. Block layout of a split-plot design with four mycorrhizal treatments as main plots and nine N-P fertilizer rates as sub-plots

x = border seedlings

o = test seedlings

distance between seedlings = 1.83m

four mycorrhizal treatments were planted 1.83 m apart. All rows were separated from each other by a row of border trees. Mycorrhizal treatments within each row were also separated by a border tree. Border trees were slash pine seedlings grown in the Container Corporation Nursery.

The seedlings were allowed to adjust to field conditions for 4 months to overcome the shock of outplanting, after which time the fertilizers were applied. The fertilizers were in a band along seedling rows 0.61 m wide on each side of the seedlings. NH_4NO_3 was the N source and concentrated superphosphate was the P source.

Physical and Chemical Properties of the Soil

Before the seedlings were planted, 20 soil cores from the 0-15 cm depth were randomly obtained from each block. The cores were combined to represent the initial soil conditions. The soil samples were air-dried and passed through a number ten mesh to remove organic debris. The following soil properties were determined:

a) pH in water and 1N KCl at 1:2 soil:solution ratio determined by a glass electrode-potentiometer after 20 min of stirring.

b) % organic matter by the Walkley-Black Method (Allison, 1965)

c) Cation exchange capacity (CEC) by 1N NH_4OAc saturation (Chapman, 1965).

d) Total N by Kjeldahl method to include nitrates (Bremner, 1965).

e) Total P by the Na_2CO_3 fusion method and the P content determined by the ammonium-molybdate-stannous chloride method (Jackson, 1958).

f) Nutrients extracted with 1N NH_4OAc at pH 4.8:

    1) P by ammonium molybdate-stannous chloride method.
    2) Al, Ca, and Mg by the atomic absorption spectrophotometer.
    3) K and Na by flame emission spectrophotometer.

g) Particle size distribution by the Buoyocous-hydrometer method (Day, 1965)

Table 1 summarizes the physical and chemical properties of the soil before the seedlings were outplanted. The soil belongs to the Myakka series -- a member of the sandy, siliceous hyperthermic family of Aeric Haplaquods (Soil Survey Staff, 1972). Soil reaction was acidic, measuring pH 4.5 (water) and 3.7 (1N KCl). Organic matter content of the soil was high (2.85%) as compared to other mineral soils. The cation exchange capacity (CEC) was low (4.6 meq/100g). Since this soil contains only 2.5% silt and 0.5% clay, the CEC was probably due mostly to organic matter. Total N and P of the top 0-15 cm layer was 0.052% and 61 ppm, respectively. Extractable P, Al, Ca, Mg, K, and Na were 2.3, 9, 124, 35, 16, and 94 ppm, respectively. Particle size distribution consisted of 97% sand, 2.5% silt, and 0.5% clay, indicating its textural classification as a "sand". The spodic horizon was located about 55 cm below the surface.

Studies of the Movement of Applied Nitrogen and Phosphorus in the Soil Profile

The loss of N and P fertilizers from the top soil was studied by collecting periodic soil samples (0-15 cm depth) at monthly intervals from the time the fertilizers were added until the seedlings were harvested. The samples were collected 0.3-0.6 m away from the base of the seedlings. Five cores were taken in each mycorrhizal-fertilizer treatment plot. These cores were combined, air-dried, and screened. Soil pH, total N, and total and extractable P were then determined using the above procedures.

To study fertilizer movement in the profile, soil sample cores were

Table 1. Physical and chemical properties of the top 0-15 cm layer of the soil prior to planting

Soil type	pH		Organic matter	CEC	Total		Extractable*						Particle size		
	H_2O	1N KCl			N	P	P	Al	Ca	Mg	K	Na	Sand	Silt	Clay
			%	meq/100g	%	ppm	----------	----------	ppm	----------	----------	----------	--------	%	--------
Myakka (fs)	4.5	3.7	2.83	4.6	.052	61	2.3	9.0	124	35	16	94	97	2.5	0.5

* Extracted with 1N NH_4OAc at pH 4.8.

randomly collected in March, 1973 and January, 1974 from under the unfertilized plot (N_0P_0) and plots fertilized with 90 kg N/ha (N_2P_0, N_2P_1, and N_2P_2) and 90 kg P/ha (N_0P_2, N_1P_2, and N_2P_2) down to the spodic horizon. These samples were processed like the others and total N, and total and extractable P were analyzed.

Rainfall Data

A record of precipitation, occurring during the experimental period, was obtained from a rain gauge located approximately 5 km from the experimental area.

Harvesting and Measuring Growth Parameters

The seedlings were harvested after 15 months and survival and growth data were obtained. The two tallest seedlings, out of the five planted mycorrhizal treatment, were harvested to measure responses to mycorrhizal treatments and/or fertilizer rates. Seedlings were removed by digging a 15-20 cm trench 0.61-1.0 m from each seedling and loosening the soil from the roots. Harvested seedlings were taken to the laboratory in separate plastic bags in an ice chest.

The seedlings were measured for shoot length (height), fresh and oven-dry weight of shoots and roots, number of secondary branches, length of the longest secondary branch, stem diameter, length of primary (tap) root, number of secondary roots, length of the longest secondary root, total fresh and oven-dry biomass of seedlings (combined weights of roots plus shoots), visual estimates of mycorrhizal roots (% mycorrhizae), and number of stem flushes.

Tissue Analyses

Roots and shoots of each seedling were separated and dried in a wind circulated oven at 70°C for 3-4 days. The dried tissues were ground in a Wiley Mill to pass a 20 mesh screen and analyzed for N, P, K, Ca, Mg, Al, Fe, Na, Mn, Cu, and Zn.

Nitrogen was analyzed from 1.0g of tissue by the Macro Kjeldahl method (Bremner, 1965). For the other nutrients, 0.5g of root tissue and 1.0g of shoot tissue were dry-ashed at 500°C in a muffle furnace and the ash was dissolved in 25 ml 0.1N HCl. Phosphorus was determined by the ascorbic acid method (Watanabe and Olsen, 1965). Calcium, Mg, Al, Fe, Mn, Cu, and Zn were determined by the atomic absorption spectrophotometer. Potassium and sodium were analyzed by flame emission spectrophotometer.

Morphological Characterization of Mycorrhizal Roots and Reisolation Experiments

Mycorrhizal roots were randomly selected from harvested seedlings. Roots were separated into distinct morphological forms based on mantle color, type or degree of branching, and general appearance. The roots were washed with tap water to remove adhering soil particles, soaked in detergent solution for 2 min, and surface sterilized in 100 ppm $HgCl_2$ solution for 3-4 min. The roots were rinsed ten times with sterile distilled water, cut aseptically into small segments, and transferred individually into test tubes containing 15 ml MMN. The roots were observed regularly for any fungal growth which was sub-cultured in Petri-dishes containing 30 ml MMN for further isolation. The mycelia were later studied under the light microscope for hyphal characteristics, presence of clamp connections, and mycelial color.

RESULTS

Movement of Applied Nitrogen and Phosphorus in the Soil Profile

The extent of loss of applied N from the surface 0-15 cm layer after 10 months is summarized in Table 2. The native total N concentration of the soil was 0.050% which was reduced to 0.047% after 10 months. With the addition of 22 kg N/ha, the total N concentration was increased from 0.050% to 0.059%. However, the N concentration was reduced drastically to 0.043% after 10 months. Additions of 90 kg N/ha in March, 1973, increased total N concentration from 0.050% to 0.081%. After 10 months, total N was reduced to the initial level of 0.050%. The data indicated that this Myakka soil does not have a strong capacity to retain N in the exchange complex as N was readily leached from the surface.

The loss of total P from the 0-15 cm layer of a Myakka soil after fertilization with 0, 22, and 90 kg P/ha is shown in Table 2. Total P concentration of the unfertilized soil was 61 ppm which did not change appreciably after 10 months in the field. Addition of 22 kg P/ha in March 1973 increased total P from 61 ppm to 68 ppm. However, this was reduced almost to the native content after 10 months. With the addition of 90 kg P/ha, the total P increased from 61 ppm to 96 ppm after fertilization. After 10 months, total P concentration was reduced to 73 ppm. This indicates that applied P was lost from the surface but a small amount was detected after 10 months.

Extractable P concentration, which is a measure of P available for

Table 2. Initial and final concentrations of total N, total P, and extractable P in the 0-15 cm layer of a Myakka (fs) soil fertilized with factorial combinations of 0, 22, and 90 kg N and P/ha

Sampling dates	Total N			Total P			Extractable P*		
	$N_0P_{\_}$	$N_1P_{\_}$	$N_2P_{\_}$	$N_{\_}P_0$	$N_{\_}P_1$	$N_{\_}P_2$	$N_{\_}P_0$	$N_{\_}P_1$	$N_{\_}P_2$
	--------%---------			----------------------ppm------------------					
March 1973	.050	.059	.081	61	68	96	2.0	8.5	34.9
January 1974	.047	.043	.050	58	63	73	1.5	3.1	8.0

* Extracted with 1N NH_4OAc at pH 4.8.

$N_0P_{\_}$ = average of plots fertilized with N_0P_0, N_0P_1, and N_0P_2.

$N_{\_}P_0$ = average of plots fertilized with N_0P_0, N_1P_0, and N_2P_0.

plant use, is shown in Table 2. The extractable P concentration of the unfertilized soil was 2.0 ppm in March, 1973 and 1.5 ppm in January, 1974. The addition of 22 kg P/ha increased the extractable P concentration from 2.0 ppm to 8.5 ppm. However, this was reduced to 3.1 ppm by January, 1974. The addition of 90 kg P/ha increased the extractable P concentration from 2.0 ppm to 34.9 ppm. This was drastically reduced to 8.0 ppm after 10 months, indicating that residual extractable P was detected on the surface soil.

Table 3 summarizes the total N content of the spodic horizon under unfertilized plots and those receiving 90 kg N/ha. Under unfertilized plots total N increased slightly from 0.062% to 0.070% after 10 months. Under plots fertilized with 90 kg N/ha, the total N concentration of the spodic horizon increased sharply from an average of 0.059% to 0.085% in 10 months.

Total and extractable P concentrations in the spodic horizon under unfertilized plots and those fertilized with 90 kg P/ha are shown in Table 3. Total and extractable P of the unfertilized plots were 70.2 and 1.8 ppm, respectively in March, 1973. After 10 months, both total and extractable P increased slightly to 74.9 and 3.0 ppm, respectively. When 90 kg P/ha was added in March, 1973, total and extractable P concentrations in the spodic horizon averaged 78 and 2.8 ppm, respectively. After 10 months, total and extractable P increased to 86.5 and 8.8 ppm, respectively.

It was evident that the N and P fertilizers were leached from the surface and were accumulated in the spodic horizon after 10 months.

Table 3. Initial and final total N, total P, and extractable P concentrations in the spodic horizon of a Myakka (fs) soil under unfertilized plots or plots receiving 90 kg N or P/ha

Sampling dates	Total N		Total P		Extractable P*	
	N_0P_0	$N_2P_{\_}$	N_0P_0	$N_{\_}P_2$	N_0P_0	$N_{\_}P_2$
	------%-------		-----------------	ppm	-----------------	
March 1973	.062	.059	70.2	78.0	1.8	2.8
January 1974	.070	.085	74.9	86.5	3.0	8.8

* Extracted with 1N NH$_4$OAc at pH 4.8.

$N_2P_{\_}$ = average of plots fertilized with N_2P_0, N_2P_1, and N_2P_2.

$N_{\_}P_2$ = average of plots fertilized with N_0P_2, N_1P_2, and N_2P_2.

Rainfall Measurements

The amount of precipitation which fell over the area during the experimental period is summarized in Table 4. A total of 182.17 cm was recorded during the entire period giving a monthly average of 11.39 cm. After the seedlings were outplanted in November, 1972, 18.06 cm fell over the area, followed by 13.05 cm in December. Precipitation was highest in July (30.62 cm) and lowest in November (1.35 cm).

Seedling Parameters Prior to Outplanting

Initial parameters of test seedlings are summarized in Table 5. No significant differences in initial height or root length of seedlings among the four mycorrhizal treatments were observed. However, oven-dry weights of roots and shoots of the UI seedlings were significantly less than all seedlings receiving TT, PT, or SN treatments. Seedlings from the SN treatment were significantly heavier than those from the other mycorrhizal treatments. Good mycorrhizal root development was obtained by TT (65%) and PT (57%) treatments. Nutrient concentrations of seedlings receiving the TT, PT, and UI treatments were similar for respective nutrients. However, nutrient concentrations in the root or shoot tissues of the SN seedlings were generally low, except for Ca, Al, and Fe in the shoots.

Survival of Seedlings in the Field

Table 6 shows the survival of seedlings receiving the four mycorrhizal treatments and nine N-P fertilizer rates after 15 months in the field. The average survival of seedlings due to mycorrhizal treatments was not significant.

Table 4. Monthly rainfall over the Austin Cary Forest during the experimental period.

Year and Month	Precipitation (cm)
1972	
November*	18.06
December	13.05
1973	
January	10.95
February	12.03
March**	18.74
April	10.72
May	12.06
June	15.20
July	30.62
August	8.80
September	9.39
October	1.65
November	1.35
December	12.09
1974	
January***	0.74
February***	6.72
Total	182.17
Monthly Average	11.39

* Seedlings outplanted in the field.
** N-P fertilizers added.
*** Seedlings harvested

Table 5. Initial growth parameters and mineral root and shoot concentrations of slash pine seedlings receiving the four mycorrhizal treatments

Mycorrhizal treatments	Height (cm)	Root length (cm)	Oven-dry weight		No. of lateral roots	Mycorrhizae (%)	N	
			Root (g)	Shoot (g)			Root	Shoot
							-----%----	
TT	21a*	15.5a	0.17b	0.69b	22b	65c	1.47	0.96
PT	18a	12.6a	0.13b	0.59b	15a	57c	1.38	1.16
UI	17a	13.3a	0.09a	0.48a	17a	0a	1.59	1.08
SN	20a	17.8a	0.43c	2.48c	21b	35b	0.98	1.00

* Different letters under each parameter represent significance as determined by the Duncan Multiple Range (DMR) test at the 5% level.

Table 5. Continued

Mycorrhizal treatments	P		K		Ca		Mg		Al	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	%								ppm	
TT	0.14	0.21	0.14	1.04	0.06	0.15	0.07	0.07	5754	300
PT	0.19	0.18	0.09	1.26	0.06	0.10	0.05	0.05	7056	350
UI	0.20	0.11	0.08	1.72	0.05	0.15	0.04	0.08	5155	350
SN	0.13	0.18	0.07	0.50	0.07	0.18	0.01	0.04	2098	725

Table 5. Continued

Mycorrhizal treatments	Fe		Na		Cu		Mn		Zn	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	ppm									
TT	2238	102	853	937	16	5	405	1205	21	48
PT	3253	124	1191	975	46	8	275	1537	24	27
UI	2448	97	1418	1073	13	5	193	2028	21	24
SN	672	185	350	850	18	4	85	261	14	24

Table 6. Survival of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Mycorrhizal treatments	Fertilizer Rates									Average
	N_0P_0	N_0P_1	N_0P_2	N_1P_0	N_1P_1	N_1P_2	N_2P_0	N_2P_1	N_2P_2	
	%									
TT	100	100	93	73	100	93	87	93	87	92 NS
PT	87	100	100	93	100	100	87	87	80	93 NS
UI	100	93	100	100	100	93	87	87	100	96 NS
SN	100	100	100	87	100	100	93	73	93	94 NS

NS = non-significant at the 5 % level.

General Growth Responses of Field Grown Seedlings

Figure 2 shows the response of pine seedlings receiving the four mycorrhizal treatments at the N_0P_0 rate. In general, TT, PT, and SN treatments caused better root and shoot development than the UI seedlings.

Fertilization with 22 kg P/ha (Figure 3) considerably improved the response of seedlings than the unfertilized seedlings (Figure 2). The TT, PT, and SN mycorrhizal treatments induced larger height and root development than the UI seedlings.

Increasing the P rate to 90 kg P/ha (Figure 4) improved the growth of seedlings receiving the TT, PT, and SN mycorrhizal treatments. The UI treatment gave poor response; needles of seedlings chlorotic, and root development largely inhibited. Root and shoot development from the TT treated seedlings were greatly increased. The effect of high P rates was evident on the root development of TT, PT, and SN treatments.

At the 22 kg N/ha (Figure 5), the seedlings receiving TT, PT, and SN treatments were significantly larger than those from the UI treatment. The growth of seedlings at this N-P rate was similar to that at the N_0P_0 (Figure 2).

Growth of seedlings receiving the four mycorrhizal treatments and fertilized with 22 kg N and P/ha is shown in Figure 6. Seedlings receiving the TT, PT, and SN treatments were larger than the UI seedlings.

Figure 7 shows the response of slash pine seedlings to 22 kg N/ha and 90 kg P/ha. Seedlings receiving the TT, PT, and SN treatments were significantly larger than the UI seedlings. Larger height responses were obtained from the TT and SN treatments. Heights of seedlings from the PT and UI treatments were the same but the former exhibited larger

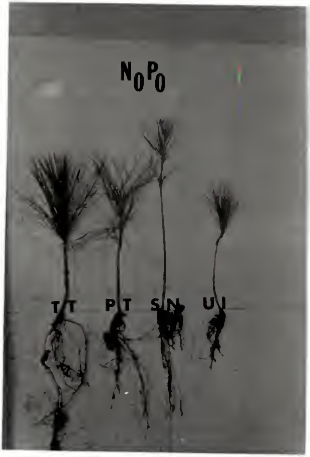

Figure 2. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_0P_0 fertilizer rate

TT = inoculated with *T. terrestris*
PT = inoculated with *P. tinctorius*
SN = standard nursery seedling
UI = uninoculated

N_0P_0 = 0 kg N/ha : 0 kg P/ha.

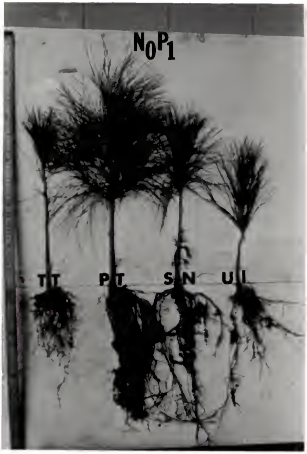

Figure 3. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_0P_1 fertilizer rate

TT = inoculated with *T. terrestris*
PT = inoculated with *P. tinctorius*
SN = standard nursery seedling
UI = uninoculated

N_0P_1 = 0 kg N/ha : 22 kg P/ha.

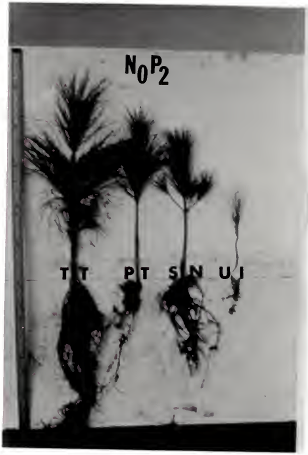

Figure 4. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_0P_2 fertilizer rate

TT = inoculated with *T. terrestris*
PT = inoculated with *P. tinctorius*
SN = standard nursery seedling
UI = uninoculated

N_0P_2 = 0 kg N/ha : 90 kg P/ha.

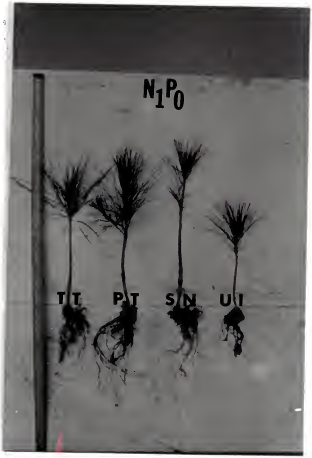

Figure 5. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_1P_0 fertilizer rate

TT = inoculated with T. terrestris
PT = inoculated with P. tinctorius
SN = standard nursery seedling
UI = uninoculated

N_1P_0 = 22 kg N/ha : 0 kg P/ha.

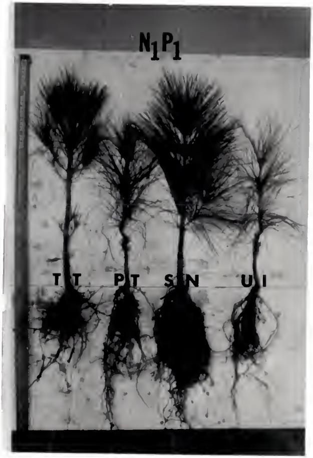

Figure 6. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_1P_1 fertilizer rate

TT = inoculated with T. terrestris
PT = inoculated with P. tinctorius
SN = standard nursery seedling
UI = uninoculated

N_1P_1 = 22 kg N/ha : 22 kg P/ha.

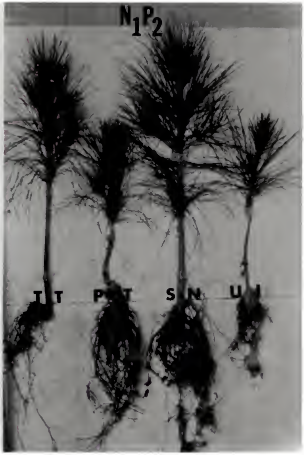

Figure 7. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_1P_2 fertilizer rate

TT = inoculated with *T. terrestris*
PT = inoculated with *P. tinctorius*
SN = standard nursery seedling
UI = uninoculated

N_1P_2 = 22 kg N/ha : 90 kg P/ha.

stem and root development than the latter. Ninety kg P/ha and 22 kg N/ha promoted root development of seedlings receiving the TT, PT, and SN treatments.

At 90 kg N/ha (Figure 8), seedlings receiving the TT, PT, and SN treatments had larger roots and shoots than that from the UI treatment. Fertilization with 90 kg N/ha significantly promoted the development of secondary branches of the seedlings receiving the TT and PT treatments.

Figure 9 shows the response of seedlings to four mycorrhizal treatments and fertilized with 90 kg N/ha and 22 kg P/ha. Heights of seedlings receiving the TT, PT, and SN treatments were significantly taller than those from the UI treatment. The high rate of N promoted secondary branch formation for seedlings treated with the TT and PT.

Height growth and root development of seedlings receiving the TT, PT, and UI treatments were significantly larger than the UI treatment at the 90 kg N/ha and 90 kg P/ha fertilizer levels (Figure 10). The TT treatment induced larger growth response than all other mycorrhizal treatments at this N-P rate. High rates of N promoted secondary branch formation as demonstrated previously at the N_2P_0 (Figure 8) or N_2P_1 (Figure 9) rates. Ninety kg P/ha significantly increased root development of seedlings receiving the TT, PT, and SN treatments than that of the UI treatment.

In general, slash pine seedlings receiving the TT, PT, and SN treatments produced better root and shoot development than those from the UI treatment at all N-P rates. Poor growth responses were obtained from unfertilized treatments. Ninety kg N/ha promoted secondary branch development, while 90 kg P/ha increased root development.

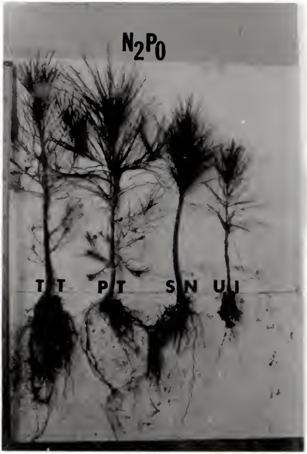

Figure 8. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_2P_0 fertilizer rate

TT = inoculated with _T. terrestris_
PT = inoculated with _P. tinctorius_
SN = standard nursery seedling
UI = uninoculated

N_2P_0 = 90 kg N/ha : 0 kg P/ha.

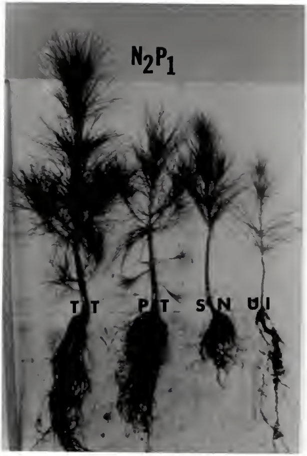

Figure 9. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_2P_1 fertilizer rate

TT = inoculated with *T. terrestris*
PT = inoculated with *P. tinctorius*
SN = standard nursery seedling
UI = uninoculated

N_2P_1 = 90 kg N/ha : 22 kg P/ha.

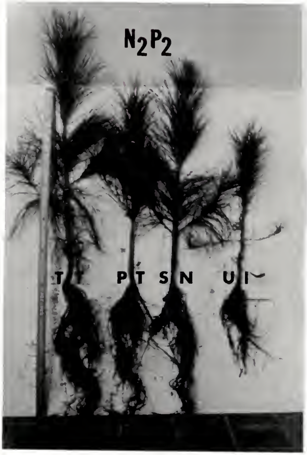

Figure 10. Response of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and N_2P_2 fertilizer rate

TT = inoculated with *T. terrestris*
PT = inoculated with *P. tinctorius*
SN = standard nursery seedling
UI = uninoculated

N_2P_2 = 90 kg N/ha : 90 kg P/ha.

Specific Growth Responses of Field Grown Seedlings

Height

Analysis of shoot length (height) of slash pine seedlings after 15 months in the field showed a highly significant response to mycorrhizal treatments and applications of N or P fertilizers (Table 7). Heights of the UI-unfertilized seedlings were lowest (21.7 cm) as compared to all other mycorrhizal-fertilizer treatments (Table 8). Heights increased as the N and P rates were increased under all mycorrhizal treatments. On the average, the SN treatment produced larger height growth (51.3 cm) than the TT (47.3 cm) or PT (41.7 cm) treatments. The UI treatment produced significantly shorter seedlings (33.9 cm) as compared to those from the other mycorrhizal treatments.

Ninety kg N/ha from NH_4NO_3 (Table 9) induced significantly longer shoot length (48.71 cm) than when N was not applied (38.75 cm). No significant difference in height was observed between the 0 and 22 or 22 and 90 kg N/ha. For P fertilization, 22 and 90 kg P/ha produced taller seedlings (45.34 and 48.37 cm, respectively) than the unfertilized seedlings (36.94 cm). The height response to different rates of N and P was linear and quadratic, respectively.

Fresh Weight of Shoots

Differences in fresh weights of shoots were significant for mycorrhizal treatments and fertilization with N or P (Table 7). Interactions between mycorrhizal treatments and P rates occurred for fresh weight of shoots. Shoots of UI-unfertilized seedlings weighed significantly less (6.3 g) as compared to all other mycorrhizal-fertilizer treatments (Table 10). For all mycorrhizal treatments, fresh weight of shoots was im-

Table 7. Analyses of variances (mean Squares) of shoot parameters of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Source	df	Shoot length	Fresh weight	Oven-dry weight	Number of secondary branches	Length of secondary branch	Stem diameter	Number of stem flushes
Blocks	2	1290.06	43781.20*	5499.83	120.19	296.70	0.42	9.56*
Mycorrhizae	3	1538.54**	27249.62**	4018.75**	133.69**	293.80**	1.35**	11.88**
Error (a)	6	115.88	7000.81	958.31	29.24	72.68	0.11	0.44
Nitrogen-L	1	1711.76**	7021.78**	1845.60**	61.04**	278.99**	1.10**	2.28*
-Q	1	83.52	1349.76	142.26	27.35*	46.98	0.01	2.46*
Phosphorus-L	1	1843.98**	29545.21**	4253.05**	226.78**	565.47**	1.88**	3.21*
-Q	1	681.19**	5126.85*	683.76**	176.11**	71.06*	0.81**	3.47*
NxP-(L x L)	1	30.47	38.50	8.01	0.20	13.01	0.02	0.53
-remainder	3	33.44	239.06	42.81	4.68	1.34	0.03	0.17
M x N	6	39.11	614.55	63.20	10.06*	54.32**	0.04	0.69
M x P	6	23.86	1846.24*	306.71**	6.79	16.59	0.04	0.70
M x N x P	12	23.67	426.19	56.77	9.99**	16.19	0.03	0.43
Error (b)	64	52.92	795.22	93.29	4.02	13.31	0.05	0.51

* Significant at the 5% level.
** Significant at the 1% level.

Table 8. Heights of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	cm			
N_0P_0	35.5	30.9	21.7	42.5
N_0P_1	43.2	38.0	32.5	48.9
N_0P_2	46.5	45.9	28.6	50.8
N_1P_0	35.7	36.7	28.3	40.0
N_1P_1	49.9	40.7	34.8	54.8
N_1P_2	51.6	46.5	43.0	59.3
N_2P_0	51.3	41.6	34.0	45.2
N_2P_1	54.0	47.9	41.8	60.6
N_2P_2	60.9	47.2	40.3	59.8
Average	47.3bc*	41.7b	33.9a	51.3c

* Difference in letters among mycorrhizal treatment means indicate significant height responses at the 5% level as determined by the DMR test.

Table 9. Effects of N and P rates and corresponding regression equation on different shoot parameters of field-grown slash pine seedlings

Element	kg per ha			Regression equation
	0	22	90	
	Height (cm)			
N	38.75a*	43.18ab	48.71b	$Y = 39.64 + .11N$
P	36.94a	45.34b	48.37b	$Y = 36.94 + .470P - .004P^2$
	Fresh weight of shoots (g)			
N	55.3a*	68.5a	76.7b	$Y = 58.95 + .24N$
P	43.6a	69.7b	87.2b	
	Oven-dry weight of shoots (g)			
N	19.53a*	24.69ab	30.04b	$Y = 20.70 + .12N$
P	16.04a	25.71b	32.51b	
	Number of secondary branches			
N	4.94a*	6.58b	7.06b	
P	3.47a	7.36b	7.75b	$Y = 3.47 + .221P - .002P^2$

* Differences in letters across N or P indicate significant responses of respective parameter to fertilizer rates at the 5 % level as determined by the DMR test.

Y = estimate of response parameter

Table 9. Continued.

Element	kg per ha			Regression equation
	0	22	90	
	Length of longest secondary branch (cm)			
N	6.88a*	9.39ab	11.11b	
P	6.05a	9.33b	11.99b	$Y = 6.05 + .176P - .001P^2$
	Stem diameter (cm)			
N	1.01a*	1.10a	1.26b	$Y = 1.02 + .003N$
P	0.91a	1.19b	1.28b	$Y = -1.03 + .123P - .001P^2$
	Number of stem flushes			
N	2.89a*	3.33b	3.33b	$Y = 2.89 + .025N - .0002N^2$
P	2.83a	3.36b	3.36b	$Y = 2.83 + .030P - .0003P^2$

* Differences in letters across N or P indicate significant responses of respective parameter to fertilizer rates at the 5% level as determined by the DMR test.

Y = estimate of response parameter

Table 10. Fresh weight of shoots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	g			
N_0P_0	26.7	25.2	6.3	75.1
N_0P_1	58.8	45.7	36.6	102.9
N_0P_2	72.3	67.6	13.7	133.3
N_1P_0	44.2	51.4	14.8	56.8
N_1P_1	65.3	66.4	32.3	123.3
N_1P_2	110.6	68.4	49.6	138.8
N_2P_0	72.8	51.3	30.6	68.1
N_2P_1	82.2	81.5	41.7	100.0
N_2P_2	130.7	69.5	39.1	153.0
Average	73.7	58.6	29.4	105.7

proved as the N and P rates were increased. On the average, fresh weight of shoots of seedlings receiving the SN (105.7 g), TT (73.7 g), and PT (58.6 g) treatments weighed significantly more than those from the UI treatment.

Fresh weight of shoots of seedlings fertilized with 90 kg N/ha (Table 9) was significantly more (76.7 g) than those fertilized with 22 kg N/ha (68.5 g) or unfertilized (55.3 g). Response of fresh weight of shoots to different N rates was linear. For P rates, 22 and 90 kg P/ha induced more fresh weight of shoots (69.7 and 87.2 g, respectively) than at the unfertilized control (43.6 g).

Interaction between mycorrhizal treatments and P rates occurred for fresh weight of shoots (Table 11). At the unfertilized treatment, fresh weight of shoots from the UI treatment was significantly less (17.2 g) than that from the TT (47.9 g) and SN (66.7 g) treatments. Fresh weight of shoots was not significantly different between the TT and UI treatments. At 22 kg P/ha, fresh weight of shoots from the UI treatment (36.9 g) was significantly less than the seedlings receiving the TT (68.8 g), and SN (108.7 g) treatments. At the 90 kg P/ha, fresh weight of seedlings receiving the four mycorrhizal treatments was significantly different among each other. The UI treatment induced the lowest fresh weight of shoots (34.1 g) as compared to the PT, TT, and SN treatments.

Fresh weight of shoots were linear for the TT and SN mycorrhizal treatments over all the P rates (Table 12). The PT and UI treatments did not interact with P rates to significantly affect the fresh weight of shoots; the response was attributed, therefore, mainly to the mycorrhizal treatment.

Table 11. Interactions between mycorrhizal treatments and P rates on various response parameters of field-grown slash pine seedlings

Mycorrhizal treatments	P rates (kg/ha)		
	0	22	90
	Fresh weight of shoots (g)		
TT	47.9b*	68.8b	104.5c
PT	42.7ab	64.5b	68.5b
UI	17.2a	36.9a	34.1a
SN	66.7b	108.7c	141.0d
	Oven-dry weight of shoots (g)		
TT	18.36bc*	25.53b	41.73c
PT	14.42ab	23.26b	23.23
UI	6.57a	13.07a	12.56a
SN	24.80c	40.99c	52.53d

* Difference in letters under all P rates indicates significant responses of respective parameters to mycorrhizal treatments at the 5% level as determined by the DMR test.

Table 11. Continued.

Mycorrhizal treatments	P rates (kg/ha) 0	22	90
	Total fresh weight (g)		
TT	72.4b*	102.0b	159.6c
PT	65.7ab	102.2b	109.0b
UI	26.9a	56.9a	53.7a
SN	96.4b	160.6c	207.4d
	Total dry weight (g)		
TT	24.78b*	34.46b	56.87c
PT	21.18ab	32.00b	32.31b
UI	9.00a	16.39a	17.06a
SN	32.57b	54.17c	69.36d

* Difference in letters under all P rates indicates significant responses of respective parameters to mycorrhizal treatments at the 5% level as determined by the DMR test.

Table 12. Interactions between mycorrhizal treatments and P rates on various response parameters of field-grown slash pine seedlings with corresponding regression equations

Mycorrhizal treatments	P rates (kg/ha) 0	22	90	Regression equation
	Fresh weight of shoots (g)			
TT	47.9a*	68.8ab	104.5b	$Y = 50.99 + .63P$
PT	42.7a	64.5a	68.5a	
UI	17.2a	36.9a	34.1a	
SN	66.7a	108.7ab	141.7b	$Y = 77.44 + .83P$
	Oven-dry weight of shoots (g)			
TT	18.36a*	25.53ab	41.73b	$Y = 18.97 + .26P$
PT	14.40a	23.26a	23.23a	
UI	6.57a	13.07a	12.56a	
SN	24.80a	40.99ab	52.53b	$Y = 24.80 + .874P - .006P^2$

* Differences in letters across mycorrhizal treatments indicate indicate significant responses of respective parameter to P rates at the 5% level as determined by the DMR test.

Y = estimate of response parameter.

Table 12. Continued.

Mycorrhizal treatments	P rates (kg/ha) 0	22	90	Regression equation
		Total fresh weight (g)		
TT	72.4a*	102.0ab	159.6b	$Y = 75.96 + .97P$
PT	65.7a	102.2a	109.0a	
UI	26.9a	56.9a	53.7a	
SN	96.4a	160.ab	207.4b	$Y = 96.39 + 3.46P - .025P^2$
		Total oven-dry weight (g)		
TT	24.78a*	34.46ab	56.87b	$Y = 25.54 + .36P$
PT	21.18a	32.00a	32.31a	
UI	9.00a	16.39a	17.06a	
SN	32.57a	54.17ab	69.36b	$Y = 32.57 + 1.17P - .008P^2$

* Differences in letters across mycorrhizal treatments indicate significant responses of respective parameter to P rates at the 5% level as determined by the DMR test.

Y = estimate of response parameter.

Oven-dry Weight of Shoots

Oven-dry weight of shoots responded significantly to mycorrhizal treatments and N and/or P fertilization (Table 7). Mycorrhizal treatments interacted with P rates to induce oven-dry weight of shoots. The dry weight of shoots of the UI-unfertilized seedlings (2.0 g) was less than that of all other mycorrhizal-fertilizer treatments (Table 13). Generally, the SN treatment induced larger oven-dry weight of shoots (39.4 g) than the TT(28.5 g), PT (20.3 g), and UI (10.7 g) treatments.For all mycorrhizal treatments, oven-dry weights of shoots were improved as the N-P rates were increased.

Ninety kg N/ha produced significantly larger dry weight of shoots (30.04 g) than the 22 kg N/ha (24.69 g) or the unfertilized treatment (19.53 g). The response of oven-dry weight of shoots to N rates was linear (Table 9). For P fertilization, dry weights of shoots at 90 and 22 kg P/ha (32.51 and 25.71 g, respectively) were significantly heavier than that at the 0 P rate (16.04 g).

Interaction between mycorrhizal treatments and P rates occurred for oven-dry weight of shoots (Table 11). At the 0 P rate, dry weight of shoots from the UI treatment (6.57 g) was significantly lesser than those from the TT, PT and SN treatments. At the 22 kg P/ha, oven-dry weight of shoots from the UI treatment (13.07 g) was significantly less than those from the TT (25.53 g), PT (23.26 g), or SN (40.99 g) treatments. At the 90 kg P/ha, response in oven-dry weight of shoots was significantly different among the four mycorrhizal treatments. Oven-dry weight of shoots of the UI treatment was significantly lower (12.56 g) than all other mycorrhizal treatments.

Oven-dry weight of shoots of seedlings receiving the mycorrhizal

Table 13. Oven-dry weights of shoots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	g			
N_0P_0	9.2	5.2	2.0	26.6
N_0P_1	21.6	16.8	12.9	37.9
N_0P_2	32.6	18.5	5.2	45.8
N_1P_0	15.8	18.4	5.4	21.2
N_1P_1	22.7	21.9	10.9	45.0
N_1P_2	42.2	25.0	18.0	49.8
N_2P_0	30.0	19.6	12.3	26.5
N_2P_1	32.3	31.1	15.4	40.1
N_2P_2	50.4	26.2	14.5	62.0
Average	28.5	20.3	10.7	39.0

treatments TT and SN gave a significant linear and quadratic response, respectively, with P rates (Table 12). The seedlings from the PT and UI treatments did not respond significantly to P rates.

Number of Secondary Branches

Mycorrhizal treatments and N or P fertilization produced a significant effect on the number of secondary branches formed (Table 7). The analysis also detected a interaction between mycorrhizal treatments and N rates. The UI-unfertilized seedlings did not produce secondary branches during the experiment (Table 14). On the average, more secondary branches were formed by seedlings receiving TT, PT, and SN treatments than those from the UI treatment. UI treatment promoted an average of only 3.75 secondary branches. The number of secondary branches increased as the N and/or P levels increased under all mycorrhizal treatments.

More secondary branches were formed at 22 and 90 kg N or P/ha than at the unfertilized treatment (Table 9). The number of secondary branches responded quadratically to all P rates.

Interaction between mycorrhizal treatments and N rates occurred for the formation of secondary branches (Table 15). At the unfertilized treatment, the SN and TT treatments formed more secondary branches (6.44 and 7.33, respectively) than those receiving the PT treatment (4.11). Significantly fewer secondary branches (1.89) were induced by the UI treatment than by the other mycorrhizal treatments. As the N rate was increased to 22 kg N/ha, more branches were formed by seedlings receiving the TT (8.89) and PT (7.33) treatments. The UI treatment formed significantly fewer secondary branches (3.33) than all mycorrhizal treatments. At 90 kg N/ha, seedlings from the TT and PT treatments

Table 14. Number of secondary branches formed on field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
N_0P_0	2	2	0	4
N_0P_1	10	5	5	7
N_0P_2	10	6	1	9
N_1P_0	5	7	1	4
N_1P_1	11	7	4	8
N_1P_2	11	8	6	8
N_2P_0	8	5	2	3
N_2P_1	7	12	6	6
N_0P_0	12	9	5	9
Average	8.48	6.74	3.15	6.41

Table 15. Interactions between mycorrhizal treatments and N rates on the responses of secondary branches of field-grown slash pine seedlings

Mycorrhizal treatments	N rates (kg/ha) 0	22	90
		Number of secondary branches	
TT	7.33c*	8.89c	9.22b
PT	4.11b	7.33bc	8.78b
UI	1.89a	3.33a	8.11a
SN	6.44c	6.78b	6.00a
		Length of longest secondary branch (cm)	
TT	7.97b*	9.29b	15.00c
PT	5.50b	11.28bc	11.59bc
UI	1.67a	4.04a	7.50a
SN	12.37c	12.94c	10.33ab

* Difference in letters under all P rates indicates significant responses of respective parameters to mycorrhizal treatments at the 5% level as determined by the DMR test.

formed more secondary branches than those from the SN or UI treatments.

Considering all N rates (Table 16), the significant response in branch formation was shown by seedlings receiving PT (quadratic response) and the UI (linear) treatments. Seedlings from the TT and SN treatments were unaffected by the different N rates and were therefore mainly a mycorrhizal response.

Length of Longest Secondary Branch

Mycorrhizal treatments and N or P fertilization significantly increased the length of the longest secondary branch (Table 7). Interaction between mycorrhizal treatments and N rates on branch length was also observed. Since the UI-unfertilized seedlings did not form secondary branches, this treatment gave no measurements for length of secondary branches as compared to other treatments (Table 17). Under all mycorrhizal treatments, length of secondary branches increased as the N and P rates were improved. Seedlings receiving TT (10.8 cm), PT (9.5 cm), and SN (11.9 cm) treatments produced longer branches than those from the UI (4.4 cm) treatment.

For N fertilization (Table 9), longer secondary branches were obtained at 90 kg N/ha (11.11 cm) than at the unfertilized treatment (6.88 cm). No significant difference in length of branches was observed between the 0 and 22 kg N/ha or 22 and 90 kg N/ha. For P rates, 22 and 90 kg P/ha produced branch lengths of 9.33 and 11.99 cm, respectively, which were significantly longer than the branches resulting when P was not applied. The response of branch lengths to P rates was quadratic.

Interactions between mycorrhizal treatments and N rates were observed for length of secondary branches. At the unfertilized treatment (Table 15), seedlings receiving the SN treatment produced longer

Table 16. Interactions between mycorrhizal treatments and N rates on various response parameters of field-grown slash pine seedlings with corresponding regression equations

Mycorrhizal treatments	N rates (kg/ha) 0	 22	 90	Regression equation
		Number of secondary branches		
TT	7.33a*	8.89a	9.22a	
PT	4.11a	7.33ab	8.78b	$Y = 4.11 + .168N - .001N^2$
UI	1.89a	3.33a	8.11b	$Y = 2.29 + .069N$
SN	6.44a	6.78a	6.00a	
		Length of longest secondary branch (cm)		
TT	7.97a*	9.29ab	15.00b	$Y = 7.77 + .08N$
PT	5.50a	11.28b	11.59b	$Y = 5.50 + .326N - .003N^2$
UI	1.67a	4.04ab	7.50b	$Y = 2.09 + .07N$
SN	12.37a	12.94a	10.33a	

* Difference in letters across mycorrhizal treatments indicate significant response of respective parameter to N rates at the 5% level as determined by the DMR test.

Table 17. Length of the longest secondary branch of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	cm			
N_0P_0	4.9	1.5	0.0	9.3
N_0P_1	6.5	6.8	4.0	11.5
N_0P_2	12.5	8.2	1.0	16.3
N_1P_0	4.9	11.3	0.8	9.2
N_1P_1	10.3	10.2	3.9	15.2
N_1P_2	12.7	12.3	7.4	14.5
N_2P_0	14.2	8.0	4.7	3.8
N_2P_1	11.8	13.3	8.5	10.0
N_2P_2	19.0	13.5	9.3	17.2
Average	10.8	9.5	4.4	17.2

branches (12.37 cm) than those from the TT (7.99 cm) and PT (5.50 cm) treatments. The UI treatment induced shorter branches (1.67 cm) than all other mycorrhizal treatments. As the N rate was increased to 22 kg N/ha, seedlings receiving the UI treatment produced significantly shorter branches than all seedlings receiving TT, PT, or SN treatments. At 90 kg N/ha, branch lengths of seedlings receiving the TT and PT treatments were longer than that from the UI treatment.

Branch length of seedlings from the TT and UI treatment responded linearly to all N rates (Table 16) while that from PT treatment responded quadratically. Seedlings receiving the SN treatment did not respond to N rates.

Stem Diameter

Stem diameter responded significantly to mycorrhizal treatments and N and/or P fertilization (Table 7). UI-unfertilized seedlings produced the smallest stem diameter (0.5 cm) than all treatments (Table 18). On the average, diameter of seedlings receiving the TT, PT, and SN treatments was significantly larger than those from the UI treatment. Diameters usually become larger as the N-P rates were increased.

Ninety kg N/ha (Table 9) induced the largest stem diameter (1.26 cm) than the 0 or 22 kg N/ha levels (1.01 and 1.10 cm, respectively). The response of stem diameter to N rates was linear. For P rates, 22 and 90 kg P/ha produced bigger stem diameter (1.19 and 1.28 cm, respectively) than when P was not applied (0.91 cm). The response of stem diameter to P rates was quadratic.

Number of Stem Flushes

Significant difference in the number of stem flushes was obtained

Table 18. Stem diameters of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer treatments

Fertilizer	Mycorrhizal Treatments			
rates	TT	PT	UI	SN
	cm			
N_0P_0	0.8	0.8	0.5	1.0
N_0P_1	1.1	1.0	0.9	1.4
N_0P_2	1.3	1.2	0.6	1.4
N_1P_0	0.9	0.9	0.6	1.0
N_1P_1	1.1	1.0	0.9	1.5
N_1P_2	1.4	1.3	1.0	1.6
N_2P_0	1.3	1.0	0.8	1.2
N_2P_1	1.4	1.5	1.0	1.4
N_2P_2	1.6	1.3	1.0	1.6
Average	1.2b*	1.1b	0.8a	1.3b

* Difference in letters among mycorrhizal treatment means indicate significant response in stem diameters at the 5% level as determined by the DMR test.

from mycorrhizal treatments and N or P fertilization (Table 7). The UI-unfertilized seedlings flushed only once during the experimental period (Table 19) as compared to multiple flushing exhibited by other treatments. On the average, the UI treatment induced fewer stem flushes (2.26) than the TT (3.78), SN (3.52), and PT (3.19) treatments.

Effects of N and P fertilization on number of flushes is summarized in Table 9. Seedlings fertilized with 22 and 90 kg N or P/ha produced more stem flushes than those which were not fertilized. Number of stem flushes exhibited a quadratic response to various rates of N or P.

Length of Primary Root

Length of primary (tap) root responded significantly to mycorrhizal treatments and fertilization with N and/or P (Table 20). The statistical analysis also showed a N and P rate interaction in the length of tap root. The UI-unfertilized seedlings generally produced shorter tap roots (16.7 cm) than all other treatment combinations (Table 21). On the average, tap roots of seedlings receiving the UI treatment (24.1 cm) were significantly shorter than those from the SN (30.3 cm), TT (27.5 cm), and PT (26.8 cm) treatments.

Tap roots of seedlings fertilized with 22 and 90 kg N or P/ha (Table 22) were significantly longer than those from the unfertilized treatment. No differences were observed in the length of tap roots between the 22 and 90 kg N or P.

The length of tap roots was influenced by interactions between N and P rates (Table 20). The analysis of variance shows that the relationship of N and P rates on length of tap root was complex; the remaining components (Linear x Quadratic, Quadratic x Linear, and Quadratic x Quadratic) being significant. Examination of the N x P interaction

Table 19. Number of stem flushes of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
N_0P_0	4	3	1	3
N_0P_1	3	3	2	4
N_0P_2	4	3	2	4
N_1P_0	3	3	2	3
N_1P_1	4	3	2	5
N_1P_2	4	4	3	4
N_2P_0	4	3	3	3
N_2P_1	4	3	3	3
N_2P_2	4	3	2	4
Average	3.78*	3.19b	2.26a	3.52bc

* Difference in letters among mycorrhizal treatment means indicate significant response in number of stem flushes at the 5% level as determined by the DMR test.

Table 20. Analyses of variances (Mean Squares) of root parameters of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Source	df	Length of tap root	Fresh weight of roots	Oven-dry weight of roots	Number of secondary roots	Length of longest secondary root	Percent mycorrhizae
Blocks	2	247.81**	2049.52	334.52	487.19**	3508.55**	913.06**
Mycorrhizae (M)	3	175.16**	4939.13*	372.91*	87.93**	5138.14**	1069.64**
Error (a)	6	12.54	801.48	65.63	6.87	270.22	63.26
Nitrogen-L	1	121.46*	5858.67**	579.38**	247.71**	4715.93**	1663.08**
-Q	1	173.00**	252.55	10.07	10.68	223.13	178.72
Phosphorus-L	1	142.52*	8573.27**	497.97**	41.65	4944.12**	1505.39**
-Q	1	109.95*	1457.75*	53.27	32.35	2215.38**	928.02*
N x P-(Lin x Lin)	1	12.91	27.77	0.08	36.88	130.15	197.16
- remainder	3	75.68*	177.60	14.99	37.24	813.47	319.24
M x N	6	16.42	173.35	13.68	8.05	183.32	81.17
M x P	6	24.51	426.22	39.78	7.22	552.15	364.46
M x N x P	12	10.54	110.15	5.98	17.91	318.52	159.69
Error (b)	64	24.20	282.35	19.61	15.84	297.49	202.71

* Significant at the 5% level.

** Significant at the 1% level.

Table 21. Lengths of primary roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	cm			
N_0P_0	23.8	21.5	16.7	21.5
N_0P_1	27.3	27.7	24.0	34.5
N_0P_2	28.0	24.7	21.6	26.8
N_1P_0	25.5	30.3	20.7	31.4
N_1P_1	24.5	28.0	25.7	30.8
N_1P_2	32.5	29.4	28.3	34.5
N_2P_0	28.8	26.5	22.2	31.3
N_2P_1	28.3	25.7	30.0	30.6
N_2P_2	29.0	27.0	27.8	31.2
Average	27.5b*	26.8b	24.1a	30.3c

* Difference in letters among mycorrhizal treatment means indicate significant response in lengths of primary roots at the 5% level as determined by the DMR test.

Table 22. Effects of N and P rates and corresponding regression equations on root parameters of field-grown slash pine seedlings

Element	kg per ha			Regression equation
	0	22	90	
	Length of primary roots (cm)			
N	24.84a*	28.48b	28.20b	
P	25.02a	28.09b	28.41b	
	Fresh weight of roots (g)			
N	25.44a*	33.41ab	43.81b	Y = 26.99 + .20N
P	21.74a	35.72b	45.20b	$Y = 21.74 + .757P - .006P^2$
	Oven-dry weight of roots (g)			
N	6.08a*	8.17a	11.74b	Y = 6.39 + .06N
P	5.84a	8.78b	11.38b	Y = 6.56 + .06P

* Differences in letters across N or P indicate significant responses of respective parameter to fertilizer rates at the 5% level as determined by the DMR test.

Y = estimate of response parameter

Table 22. Continued.

Element	kg per ha 0	 22	 90	Regression equation
	Number of secondary roots			
N	17.31a*	18.94ab	21.08b	$Y = 17.63 + .04N$
P	17.94a	19.61a	19.78a	
	Length of longest secondary root (cm)			
N	56.71a*	64.01ab	73.24b	$Y = 58.17 + .18N$
P	53.40a	68.15b	72.40b	$Y = 53.40 + .819P - .007P^2$
	Ectomycorrhizal root formation (%)			
N	53.89a*	53.14a	62.25b	$Y = 52.58 + .09N$
P	49.78a	58.94a	60.56b	$Y = 49.78 + .511P - .004P^2$

* Differences in letter across N or P indicate significant responses of respective parameter to fertilizer rates at the 5% level as determined by the DMR test.

Y = estimate of response parameter

means (Table 23) revealed that longer tap root was obtained from 90 kg P/ha and 22 kg N/ha.

Fresh Weight of Roots

Mycorrhizal treatments and N or P fertilization produced significant increase of fresh weight of roots (Table 20). Fresh weight of roots of the UI-unfertilized seedlings (3.5 g) was much lower than for all other treatments (Table 24). On the average, fresh weights of seedlings receiving the UI treatment were significantly lesser than those from the SN, TT, and PT treatments. Under all mycorrhizal treatments, fresh weights of roots were improved as the N-P rates were increased.

For N fertilization (Table 22) 90 kg N/ha produced more fresh weight of roots (43.81 g) than when N was not applied (25.44 g). Fresh weight of roots responded linearly to N rates. No significant difference in fresh weight of roots was obtained from the 0 and 22 kg N/ha or from the 22 and 90 kg N/ha. For P rates, 22 and 90 kg P/ha induced significantly more fresh weight of roots (35.72 g and 45.2 g, respectively) than when P was not applied (21.74 g). The response of fresh weight of shoots to P rates was quadratic.

Oven-dry Weight of Roots

Oven-dry weight of roots responded significantly to mycorrhizal treatments and to fertilization with N or P (Table 20). Uninoculated and unfertilized seedlings produced less dry weight of roots (0.6 g) than all other treatments (Table 25). On the average, dry weights of roots of seedlings receiving the SN (12.6 g) and TT (10.1 g) treatments were significantly heavier than those from the UI (3.8 g). For all mycorrhizal treatments, oven-dry weight of roots became heavier as the N-P

Table 23. Interactions between N and P rates on length of primary root of field-grown slash pine seedlings

N rates (kg/ha)	P rates (kg/ha) 0	22	90
	------------	cm	------------
0	20.88	28.38	25.28
22	26.98	27.25	31.19
90	27.19	28.65	28.75

Table 24. Fresh weights of roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	g			
N_0P_0	11.6	11.5	3.5	26.6
N_0P_1	24.1	30.8	17.6	48.6
N_0P_2	41.5	26.1	7.0	56.1
N_1P_0	17.8	26.0	7.8	26.7
N_1P_1	27.7	27.6	14.9	57.7
N_1P_2	57.9	42.8	28.2	62.7
N_2P_0	44.0	31.8	17.8	32.5
N_2P_1	47.8	54.8	27.7	49.3
N_2P_2	65.7	52.8	23.4	78.2
Average	37.6b*	33.8ab	16.4a	49.1b

* Difference in letters among mycorrhizal treatment means indicate significant response in fresh weights of roots at the 5% level as determined by the DMR test.

Table 25. Oven-dry weights of roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	g			
N_0P_0	2.6	5.1	0.6	5.5
N_0P_1	5.5	6.9	3.8	11.4
N_0P_2	11.4	5.2	1.5	13.5
N_1P_0	4.1	5.8	1.7	8.1
N_1P_1	7.1	5.9	3.2	13.7
N_1P_2	15.3	9.9	7.0	16.1
N_2P_0	12.6	9.4	5.0	9.6
N_2P_1	13.6	13.4	6.3	14.4
N_2P_2	18.6	12.1	5.0	20.8
Average	10.1b*	8.2ab	3.8a	12.6b

* Difference in letters among mycorrhizal treatment means indicate significant response in oven-dry weights of roots at the 5% level as determined by the DMR test.

rates were increased.

Comparing N rates (Table 22), 90 kg N/ha produced significantly heavier dry weight of roots (11.74 g) than the 0 and 22 kg N/ha (6.08 and 8.17 g, respectively). For P rates, 22 and 90 kg P/ha induced significantly heavier root dry weights than the unfertilized treatment. Oven-dry weight of roots responded linearly to both N and P rates.

Number of Secondary Roots

Number of secondary roots responded significantly to mycorrhizal treatments and N fertilization (Table 20). On the average, seedlings receiving the TT, PT, and SN treatments produced more secondary roots than those from the UI treatment.

For N rates (Table 22), 90 kg N/ha promoted more secondary roots (21.08) than the unfertilized treatment (17.31). Number of secondary roots responded linearly to N rates. Phosphorus rates did not affect the number of secondary roots.

Length of Longest Secondary Root

Length of the longest secondary root responded significantly to mycorrhizal treatments and N or P fertilization (Table 20). Length of secondary roots of the UI-unfertilized seedlings (21.7 cm) was significantly shorter than all other mycorrhizal-fertilizer treatments (Table 27). On the average, secondary roots of seedlings receiving the TT, PT, and SN treatments were significantly longer than those from the UI treatments. For all mycorrhizal treatments, lengths of secondary roots were improved as the N-P fertilizer rates increased.

For N rates (Table 22), 90 kg N/ha induced longer secondary roots (73.24 cm) than the 0 or 22 N rates. No significant difference

Table 26. Number of secondary roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
N_0P_0	19	16	14	21
N_0P_1	16	17	15	17
N_0P_2	20	19	14	21
N_1P_0	17	19	17	20
N_1P_1	21	19	18	24
N_1P_2	18	21	17	18
N_2P_0	20	17	17	18
N_2P_1	26	26	15	22
N_2P_2	21	24	22	24
Average	20b*	20b	17a	21b

* Difference in letters among mycorrhizal treatment means indicate significant difference in number of secondary roots at the 5% level as determined by the DMR test.

Table 27. Length of longest secondary roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments TT	 PT	 UI	 SN
	cm			
N_0P_0	57.8	54.0	21.7	62.2
N_0P_1	63.7	64.0	52.0	81.2
N_0P_2	69.5	55.5	31.7	67.3
N_1P_0	47.7	61.0	34.7	46.8
N_1P_1	67.7	56.3	46.0	89.3
N_1P_2	98.3	75.8	62.8	81.7
N_2P_0	95.0	55.0	41.8	63.2
N_2P_1	69.5	81.3	66.8	80.0
N_2P_2	106.3	79.2	48.8	91.8
Average	75.1b*	64.7b	45.2a	73.7b

* Difference in letters among mycorrhizal treatment means indicate significant response in length of longest secondary roots at the 5% level as determined by the DMR test.

in the length of secondary roots was observed between the 0 and 22 kg N/ha or 22 and 90 kg N/ha treatments. The response of secondary root extension to N rates was linear. For P rates, 22 and 90 kg P/ha produced significantly longer secondary roots (68.15 and 72.40 cm, respectively) than when P was not applied (53.40 cm). Response of length of secondary roots to P rates was quadratic.

Percent Mycorrhizae

Ectomycorrhizal root development responded significantly to mycorrhizal treatments and N or P fertilization (Table 20). The UI-unfertilized seedlings had fewer mycorrhizal roots (30%) than all other treatment combinations (Table 28). On the average, mycorrhizal roots were more in seedlings receiving the PT (65%),SN (58%), and TT (53%) than those from the UI (50%) treatments. Mycorrhizal root formation increased as the N-P fertilizer rates were elevated.

For N and P rates (Table 22), 90 kg N or P/ha promoted more mycorrhizal root formation than the 0 or 22 kg N or P/ha. Mycorrhizal formation responded linearly to N rates and quadratically to P rates.

Total Fresh Biomass

Total fresh biomass (fresh weight of roots plus shoots) responded significantly to mycorrhizal treatments and fertilization with N and/or P (Table 29). Total fresh weight was affected further by interactions between mycorrhizal treatments and P rates. Total fresh weight of the UI-unfertilized seedlings (9.8 g) was less than that from other mycorrhizal-fertilizer treatments (Table 30). On the average, total fresh weight of seedlings receiving the UI treatment (45.8 g) was significantly less than seedlings from the SN (154.8 g), TT (111.3 g) and PT

Table 28. Percent mycorrhizal roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	%			
N_0P_0	47	48	30	45
N_0P_1	44	70	67	64
N_0P_2	66	64	41	58
N_1P_0	45	55	34	51
N_1P_1	42	57	55	59
N_1P_2	50	73	57	59
N_2P_0	70	69	50	53
N_2P_1	60	69	50	53
N_2P_2	56	76	52	74
Average	53ab*	65c	50a	58b

* Difference in letters among mycorrhizal treatment means indicate significant difference in percent mycorrhizal roots at the 5% level as determined by the DMR test.

Table 29. Analyses of variances (Mean Squares) of total fresh and oven-dry weights of field-grown slash pine seedlings receiving four mycorrhizal treatments and nine N-P fertilizer rates

Source	df	Total fresh weight	Total oven-dry weight
Blocks	2	64678.05*	8565.66*
Mycorrhizae (M)	3	55057.30**	6928.38**
Error (a)	6	12422.03	1489.58
Nitrogen - L	1	25687.09**	4608.98**
- Q	1	2771.75	264.00
Phosphorus - L	1	69914.29**	7724.85**
- Q	1	12055.80*	1045.00**
N x P - (Lin x Lin)	1	129.58	4.67
- remainder	3	697.33	82.63
M x N	6	1326.56	114.06
M x P	6	3994.97*	557.06**
M x N x P	12	791.90	82.93
Error (b)	64	1727.48	169.45

* Significant at the 5% level.

** Significant at the 1% level.

Table 30. Total fresh weights of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	g			
N_0P_0	38.3	36.7	9.8	101.7
N_0P_1	82.9	76.5	54.2	151.5
N_0P_2	113.8	93.7	20.7	189.4
N_1P_0	62.0	77.4	22.6	86.8
N_1P_1	93.0	94.0	47.2	181.1
N_1P_2	168.5	111.2	77.8	201.5
N_2P_0	116.8	83.1	48.4	100.7
N_2P_1	130.0	136.3	69.4	149.3
N_2P_2	196.4	122.7	62.5	231.2
Average	111.3	92.3	45.8	154.8

(92.3 g) treatments. For all mycorrhizal treatments, total fresh weights were improved as the N-P rates increased.

For N rates (Table 31), 90 kg N/ha produced heavier total fresh weight of seedlings (120.5 g) than the unfertilized treatment (80.8 g). The response of total fresh weight to N rates was linear. For P rates, total fresh weights at 22 and 90 kg P/ha (105.4 and 132.4 g, respectively) were significantly heavier than when P was not applied (65.4 g).

Interaction between mycorrhizal treatments and P rates on total fresh weight of seedlings was observed (Table 11). At the unfertilized treatment, total fresh weights of seedlings receiving the SN and TT treatments (96.4 and 72.4 g, respectively) were significantly heavier than those from the UI treatment (26.9 g). At 22 kg P/ha, total fresh weights of seedlings from the UI treatment were significantly less (56.9 g) than those from other mycorrhizal treatments. At the 90 kg P/ ha treatment, total fresh weight was significantly different among all mycorrhizal treatments. Total fresh weight of seedlings receiving the SN, TT, and PT treatment was significantly higher than that from the UI treatment.

The TT and PT treatments induced significantly higher total fresh weight of seedlings over all P rates (Table 12). Total fresh weight response of seedlings receiving the PT and UI treatments was not significant.

Total Dry Biomass

Total dry biomass (oven-dry weight of roots plus shoots) responded significantly to mycorrhizal treatments and fertilization with N or P (Table 29). The analysis further detected a mycorrhizae x phosphorus treatment interactions for total dry weight of seedlings. The UI-

Table 31. Effects of N and P rates and corresponding regression equation on total fresh and oven-dry weights of field-grown slash pine seedlings

Element	kg per ha 0	22	90	Regression equation
		Total fresh weight (g)		
N	80.8a*	101.9ab	120.5b	Y = 85.94 + .44N
P	65.4a	105.4b	132.4b	
		Total oven-dry weight (g)		
N	25.34a*	32.91ab	41.78b	Y = 26.94 +.18N
P	21.88a	43.25b	43.90b	

* Differences in letters across N or P indicate significant responses of respective parameter to fertilizer rates at the 5% level as determined by the DMR test

Y = response parameter

unfertilized seedlings produced the lowest total dry weight (2.6 g) as compared to all other treatments (Table 32). On the average, total dry weight was significantly higher for seedlings receiving the TT, PT, and SN treatments (38.7, 28.5, and 52.0 g, respectively) than those from the UI (14.2 g) treatment. Total dry weights usually increased as the N-P rates were raised.

Nitrogen or P fertilization had highly significant effects on total dry weight of seedlings (Table 31). For N rates, 90 kg N/ha produced significantly heavier seedlings (41.78 g) than the unfertilized treatment (25.34 g). No significant dry weight response was detected between 0 and 22 kg N/ha. The response of total dry weight to N rates was linear. For P rates, 22 and 90 kg P/ha induced heavier total dry weight than when P was not applied (21.88 g).

Interactions between mycorrhizal treatments and P rates were significant to total dry weight response (Table 11). At the unfertilized treatment, total dry weights of seedlings from the SN and TT treatments (32.57 and 24.78 g, respectively) were significantly higher than that from the UI (9.00 g) treatment. At 22 kg P/ha, total dry weights of seedlings from the UI treatment was significantly lower than that from the TT, PT, or SN treatments. Increasing the P rate to 90 kg P/ha, total dry weights were significantly different among the four mycorrhizal treatments. The SN treatment induced the largest total dry weight of seedlings (69.36 g) followed by those treated with TT (56.87 g), PT (32.3 g), and UI (17.06 g).

Over all P rates (Table 12), the TT and SN treatments produced heavier oven-dry weight in seedlings than the PT or UI treatments. The seedlings treated with TT responded linearly to P rates while those

Table 32. Total dry weights of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments			
	TT	PT	UI	SN
	g			
N_0P_0	11.8	10.3	2.6	32.2
N_0P_1	27.1	23.6	13.4	49.3
N_0P_2	44.1	23.7	6.7	59.3
N_1P_0	23.0	24.2	7.1	29.4
N_1P_1	30.3	27.8	14.1	58.7
N_1P_2	57.5	35.0	25.0	65.9
N_2P_0	42.7	29.0	17.3	36.2
N_2P_1	45.9	44.6	21.7	54.5
N_2P_2	69.0	38.3	19.5	82.8
Average	38.7	28.5	14.2	52.0

receiving the SN treatment responded quadratically. Oven-dry weights of seedlings receiving the PT and UI treatments did not show a significant response to P rates.

Tissue Analyses

Nitrogen

Nitrogen concentrations of root and shoot tissues of field-grown slash pine seedlings receiving the four mycorrhizal treatments and nine N-P fertilizer rates are shown in Table 33. Shoot tissues contained more N than root tissues for all treatments. Nitrogen concentration of tissues generally improved as the N rates increased, except for seedlings treated with the TT or SN. The N concentration in the tissues of these seedlings decreased with increasing rates of N fertilizers. On the average, N concentrations of root or shoot tissues among the four mycorrhizal treatments were not different.

Total N accumulation by pine tissues is presented in Table 34. The accumulation of N by shoots was greater than in the root tissues. Tissues of the UI-unfertilized seedlings showed less N accumulation than tissues from other mycorrhizal-fertilizer treatment. Nitrogen accumulation increased as the N-P rates were elevated. On the average, N accumulation by seedlings receiving the UI treatment was lesser than those from the TT, PT, or SN treatments.

Phosphorus

Table 35 summarizes the P concentrations in root and shoot tissues of slash pine seedlings receiving the four mycorrhizal treatments and nine N-P fertilizer rates. Roots usually have higher P concentration than the shoot tissues. Under all mycorrhizal treatments, P concentration

Table 33. Nitrogen concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	%							
N_0P_0	0.53	0.74	0.66	0.98	0.47	0.51	0.70	0.78
N_1P_0	0.56	0.83	0.55	0.86	0.54	0.80	0.54	0.70
N_2P_0	0.78	1.01	0.62	1.09	1.05	1.77	0.84	1.06
N_0P_1	0.56	0.81	0.93	1.07	0.98	1.12	0.85	0.97
N_1P_1	0.44	0.70	0.66	0.98	0.39	0.66	0.56	0.81
N_2P_1	0.59	0.97	0.89	1.13	0.81	1.12	0.74	0.95
N_0P_2	1.02	0.98	0.46	0.62	0.42	0.62	0.85	1.12
N_1P_2	0.75	1.02	0.85	1.06	0.63	1.00	0.50	0.90
N_2P_2	0.62	1.02	0.96	1.26	0.70	0.87	0.54	0.83
Average	0.65	0.90	0.73	1.00	0.67	0.94	0.64	0.90

Table 34. Total N accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	mg N/root or shoot							
N_0P_0	13.8	68.1	33.7	51.0	2.8	10.2	38.5	207.5
N_1P_0	23.0	131.1	31.9	158.2	9.2	43.2	43.7	148.4
N_2P_0	98.3	303.0	58.3	213.6	52.3	217.7	80.6	280.9
N_0P_1	30.8	175.0	64.2	179.8	37.2	144.5	96.9	367.6
N_1P_1	31.2	158.9	38.9	214.6	12.5	71.9	76.7	364.5
N_2P_1	80.2	313.3	119.3	351.4	51.0	171.7	106.6	381.0
N_0P_2	116.3	319.5	23.9	114.7	6.3	32.2	114.8	510.9
N_1P_2	114.8	430.4	84.2	265.0	44.1	180.0	80.5	448.2
N_2P_2	115.3	514.1	116.2	330.1	35.0	126.2	112.3	514.6
Average	69.3	218.2	63.4	172.0	27.8	110.8	83.4	358.2

Table 35. Phosphorus concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	%							
N_0P_0	.14	.10	.13	.12	.06	.07	.11	.10
N_0P_1	.18	.15	.28	.16	.37	.16	.26	.13
N_0P_2	.35	.22	.32	.19	.30	.18	.32	.18
N_1P_0	.07	.08	.09	.09	.11	.08	.08	.08
N_1P_1	.28	.15	.30	.19	.24	.18	.29	.16
N_1P_2	.32	.20	.35	.18	.33	.20	.26	.18
N_2P_0	.19	.15	.16	.13	.15	.13	.17	.14
N_2P_1	.22	.14	.26	.13	.17	.16	.25	.14
N_2P_2	.27	.16	.30	.17	.34	.18	.25	.13
Average	.22	.15	.24	.15	.23	.15	.22	.14

of either root or shoot tissues improved as the P rates were increased. No definite pattern in P concentration of tissues was observed as the N rates were increased. On the average, P concentrations of root or shoot tissues among the four mycorrhizal treatments were not different.

Total P accumulation by pine tissues is shown in Table 36. More P was accumulated in the shoot tissues than in root tissues. Accumulation of P by roots or shoots of the UI-unfertilized seedlings was markedly less than for other mycorrhizal-fertilizer treatments. Phosphorus accumulation by tissues under all mycorrhizal treatments increased as the N-P fertilizer rates increased. Phosphorus accumulation was lowest by seedlings receiving the UI treatment than by those from the SN, TT, and PT treatments.

Potassium, Calcium, and Magnesium

Potassium, Ca, and Mg concentrations in roots and shoots are summarized in Appendices 1, 2, and 3, respectively. These three nutrients were usually higher in the shoot tissues than in the root tissues under all mycorrhizal treatments. Potassium, Ca, and Mg concentrations in the root and shoot tissues tended to increase as the N-P fertilizer rates increased. On the average, K, Ca, and Mg concentrations in roots and shoots were not different among the four mycorrhizal treatments.

Total accumulation of K, Ca, and Mg by roots and shoots are shown in Appendices 4, 5, and 6, respectively. Lower accumulations of these three nutrients by root and shoot tissues of the UI-unfertilized seedlings were observed. On the average, accumulation of the three nutrients in tissues was low by seedlings receiving the UI treatment as compared to those receiving the TT, PT, and SN treatments.

Table 36. Total P accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	mg P/root or shoot							
N_0P_0	3.6	9.2	6.6	6.4	0.4	1.4	6.1	27.5
N_0P_1	9.9	33.1	19.3	27.4	14.1	21.1	29.6	48.0
N_0P_2	39.9	72.8	16.6	35.2	4.5	9.5	43.2	82.4
N_1P_0	2.9	12.6	5.2	17.2	1.9	4.1	6.5	17.0
N_1P_1	19.9	33.3	17.7	40.9	7.7	19.6	39.7	73.5
N_1P_2	49.0	84.4	34.7	45.8	23.1	36.6	41.9	89.6
N_2P_0	23.9	45.0	15.0	26.1	7.5	15.6	16.3	37.1
N_2P_1	29.9	45.2	34.8	41.5	10.7	24.1	36.0	57.5
N_2P_2	50.2	80.6	36.3	45.4	17.0	25.6	52.0	82.7
Average	28.8	46.2	20.7	31.8	9.7	17.5	30.1	57.3

Aluminum and Iron

Aluminum and Fe concentrations in slash pine tissues are summarized in Appendices 7 and 8, respectively. Aluminum and Fe concentrations were higher in root tissues than in root tissues. No clear trends in the concentrations of Al and Fe in root or shoot tissues were observed as the N-P fertilizer rates were increased.

Total Al and Fe accumulations by root and shoot tissues are presented in Appendices 9 and 10, respectively. Roots and shoots of the UI seedlings accumulated low quantities of Al and Fe than did the seedlings receiving the TT, PT, and SN treatments. Accumulation of Al and Fe by roots or shoots under all mycorrhizal treatments usually increased as the N-P fertilizer rates were raised.

Sodium and Copper

Concentrations of Na and Cu in pine tissues are shown in Appendices 11 and 12, respectively. Roots have more Na and Cu than did shoot tissues under all mycorrhizal treatments. No definite trends in Na and Cu concentrations for either roots or shoots were observed, as the N-P fertilizer rates were increased. On the average, Na and Cu concentrations of root or shoot tissues were not different among the four mycorrhizal treatments.

Total accumulation of Na and Cu by pine tissues is summarized in Appendices 13 and 14, respectively. Large accumulation of Na and Cu by the shoot tissues occurred than by the root tissues. The UI-unfertilized seedlings accumulated the lowest amount of Na and Cu in either roots or shoots than those from other treatments. Under all mycorrhizal treatments, accumulation of Na and Cu by both roots and shoots increased as the N-P fertilizer rates increased. Among mycorrhizal treatments, the UI seedlings accumulated the least amount of Na and Cu than did the seedlings receiving TT, PT, or SN treatments.

Manganese and Zinc

Appendices 15 and 16 summarize the Mn and Zn concentrations, respectively, in roots and shoots of field-grown slash pine seedlings. Manganese and Zn concentrations are usually higher in shoots than in roots. No definite pattern was observed in the Mn and Zn concentrations in both roots and shoots, as the N-P fertilizer rates were increased. On the average, Mn and Zn concentrations in roots and shoots were not different among the four mycorrhizal treatments.

Total accumulation of Mn and Zn by pine tissues is summarized in Appendices 17 and 18, respectively. Shoots accumulated more Mn and Zn than did the roots. The UI-unfertilized seedlings accumulated the lowest amount of Mn and Zn by both root and shoot tissues. Under all mycorrhizal treatments, accumulation of Mn and Zn by roots and shoots increased as the N-P fertilizer rates were raised. On the average, the UI seedlings accumulated the least amount of Mn and Zn than did the seedlings receiving the remaining mycorrhizal treatments.

Morphological Characterization of Ectomycorrhizal Roots and Reisolation Studies

Thirteen morphological forms of ectomycorrhizal roots were observed from seedlings receiving the TT, PT, SN, or UI treatments. These forms were different from each other with respect to the mode and degree of mycorrhizal rooting, color of the fungal mantle, and the general appearance of the ectomycorrhizal roots.

Forms A, B, and C had simple or dichotomous roots. The color of the fungal mantle of Form A was predominantly brown (Figure 11). The fungal

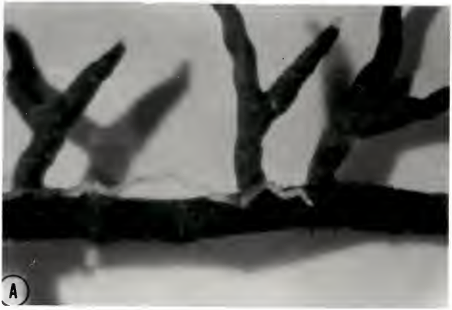

Figure 11. Form A ectomycorrhizae with simple dichotomous roots and brown fungal mantle (90 X).

mantle of Form B (Figure 12) was brown, however, the mycorrhizal roots showed constrictions giving a "beaded" appearance. The base of the roots of Form C (Figure 13) was black, while the terminal roots were light brown. Forms A, B, or C were obtained frequently from seedlings receiving the TT, PT, or SN treatments, but occassionally from UI seedlings.

Forms D and E had dichotomous or coralloid root patterns. The base of the root of Form D (Figure 14) was dark brown, while the terminal roots were black. The terminal mycorrhizal roots were broad on the sides, gradually tapering towards the base, giving the roots a clavate appearance. Form E (Figure 15) was similar to Form D in the color of the fungal mantle; however, the base of the root was white and very succulent, while the terminal roots were distinctly black. Constrictions were formed on some of the roots giving a beaded appearance. Forms D and E were obtained predominantly from seedlings receiving the SN or UI treatments and rarely from the TT or PT treatments.

Forms F, G, and H were sessile type of ectomycorrhizal roots, with no evident stalk supporting the mycorrhizal roots. The mycorrhizal roots appeared to be flat with the surface of secondary roots. Form F (Figure 16) had short mycorrhizal roots and white fungal mantle. This form was usually obtained near the tips of secondary roots. For Form G (Figure 17), the color of the fungal mantle was white; however, the mycorrhizal roots were numerous and much longer than Form F. Form H (Figure 18) was similar to Form G in rooting pattern; however, the fungal mantle was yellow-orange in color. Forms F and G were obtained from seedlings receiving the TT and SN treatments but occassionally from seedlings of the PT or UI treatments. Form H was obtained from seedlings

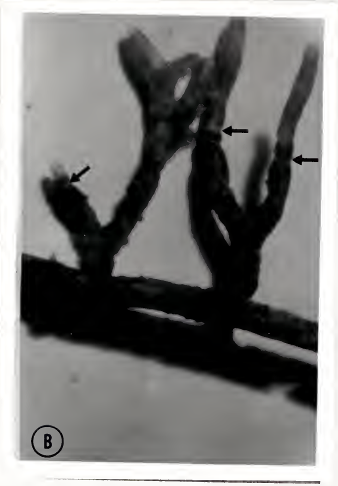

Figure 12. Form B ectomycorrhizae with simple dichotomous roots, brown fungal mantle, and typical beaded appearance. Arrows indicate constrictions on the mycorrhizal roots. (90 X).

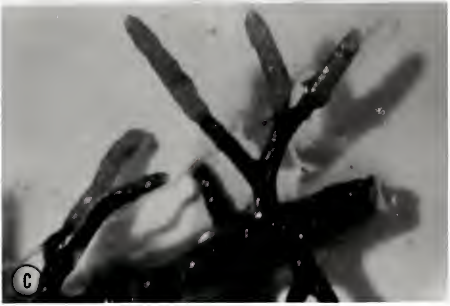

Figure 13. Form C ectomycorrhizae with simple dichotomous roots, black basal roots, and light brown fungal mantle. (90 X).

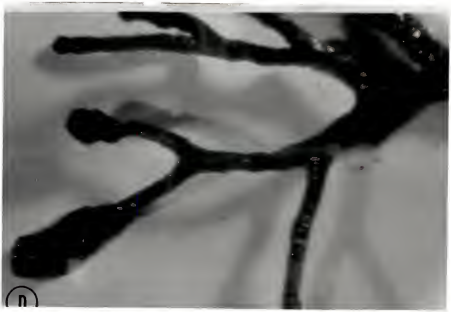

Figure 14. Form D ectomycorrhizae with dichotomous or coralloid branches, a distinctive black fungal mantle, and typical clavate-shaped terminal roots. (90 X).

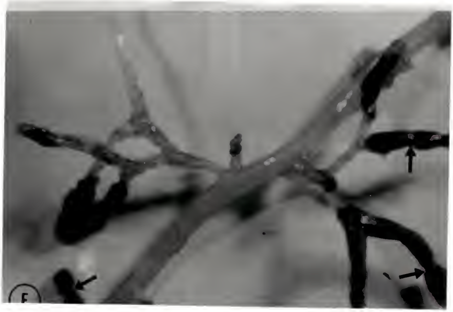

Figure 15. Form E ectomycorrhizae with dichotomous or coralloid roots and black fungal mantle. Arrows indicate constrictions on the roots giving a beaded appearance. (90 X).

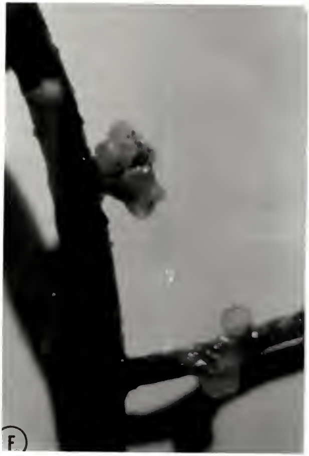

Figure 16. Form F ectomycorrhizae with typically sessiled roots and white fungal mantle. (90 X).

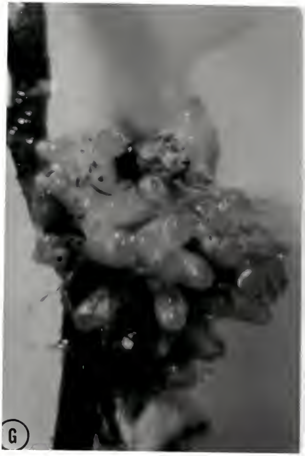

Figure 17. Form G ectomycorrhizae which are sessile, with white fungal mantle, and longer mycorrhizal roots. (90 X).

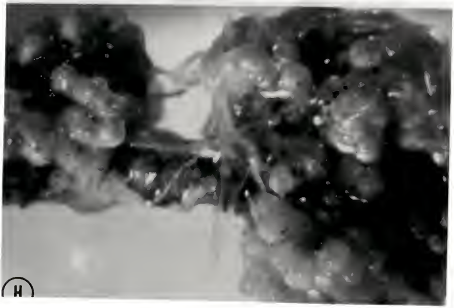

Figure 18. Form H ectomycorrhizae which are sessile and with yellow-orange fungal mantle. (90 X).

inoculated with P. tinctorius.

Form I (Figure 19) had a densely-coralloid rooting pattern similar to Forms G and H but the mycorrhizal roots formed a distinct stalk. The color of the fungal mantle was white, yellow, or brown. This form was obtained commonly from seedlings receiving the TT, PT, or SN treatments, but occassionally from the UI treatment.

Forms J, K, and L had compound-coralloid rooting patterns. The main difference among these forms was the color of the fungal mantle. Form J (Figure 20) had dark brown fungal mantle. The base of the mycorrhizal roots of Form K (Figure 21) was black and the terminal roots were white. The base of the mycorrhizal roots of Form L (Figure 22) was gray to light purple and the terminal mycorrhizal roots were white to light brown. Forms J and K were obtained usually from seedlings receiving the TT, PT, and SN treatments, but occassionally from UI seedlings.

Form M (Figure 23) had a dense-coralloid rooting pattern which tended to conglomerate into clumps of mycorrhizal roots. A sticky substance was secreted from the roots which forms a sand coating around the mycorrhizal roots. The color of the fungal mantle was predominantly brown. Form M was obtained usually from seedlings receiving the TT, PT, or SN treatments, but rarely from UI seedlings.

A total of six different fungi (Table 37) were isolated from various morphological forms of ectomycorrhizal roots. Mycelia of all six fungi were septate. Clamp connections were observed in some species.

Isolate 1 was obtained from eight different morphological forms (Table 37) and was the most frequently isolated fungus. The color of the external mycelium was white. Clamp connections (Figure 24) were commonly seen. Comparison of the mycelia of this fungus with pure cul-

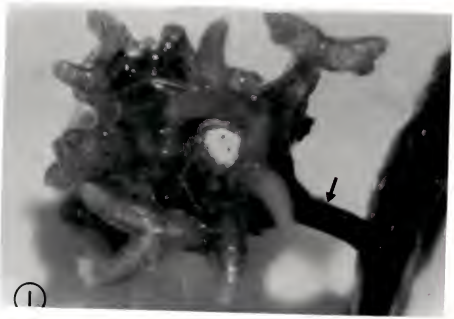

Figure 19. Form I ectomycorrhizae which are supported on stalks (arrow), and fungal mantle appearing white, yellow, or brown. (90 X).

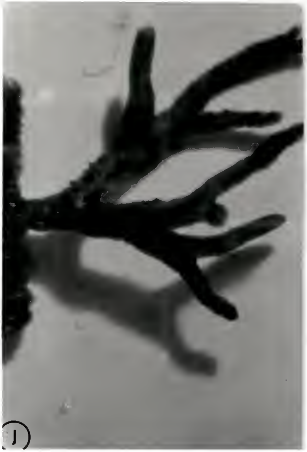

Figure 20. Form J ectomycorrhizae with compound-coralloid roots and brown fungal mantle. (90 X).

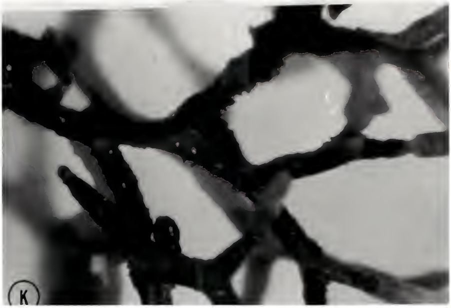

Figure 21. Form K ectomycorrhizae with compound-coralloid roots, black basal roots, and brown terminal roots. (90 X).

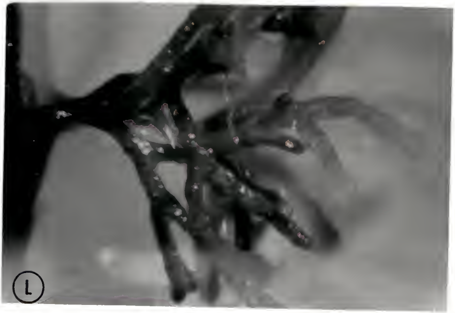

Figure 22. Form L ectomycorrhizae with compound-coralloid roots, grayish-purple basal roots, and whitish brown terminal roots. (90 X).

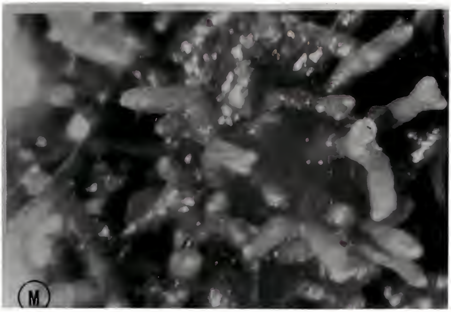

Figure 23. Form M ectomycorrhizae with densely coralloid branches, forming clumps of roots, and with brown fungal mantle. (90 X).

Table 37. Isolation of possible ectomycorrhizal fungi from different morphological forms of ectomycorrhizal roots of field-grown slash pine seedlings receiving four initial mycorrhizal treatments

Isolate number	Identification	Morphological forms
1	Thelephora terrestris	A, B, C, F, G, I, J, K
2	Pisolithus tinctorius	A, C, H, I, K
3	Cenococcum graniforme	D, J
4	Cenococcum graniforme	D, E
5	Laccaria laccata	L
6	Unidentified	B, H, I, K

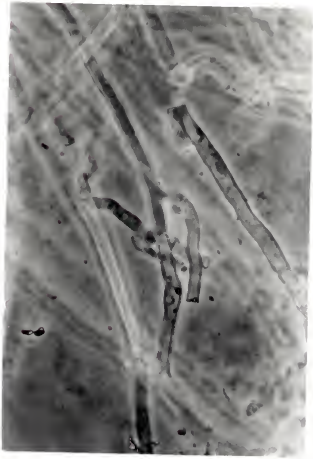

Figure 24. Microscopic characteristics of mycelia of isolate 1 showing clamp connections. (Identified as *Thelephora terrestris*). 1,200 X.

tures of known ectomycorrhizal fungi matched it closely with that of Thelephora terrestris in microscopic characteristics. This fungus was isolated from mycorrhizal roots of seedlings previously receiving the TT, PT, SN, and UI treatments.

Isolate 2 was obtained from five different morphological forms (Table 37). Color of the hyphae was yellow, identical to that of Pisolithus tinctorius. Numerous clamp connections (Figure 25) were observed. Isolate 2 was obtained from roots previously treated with PT and UI.

Isolate 3 (Figure 26) was obtained only from two morphological forms (Table 37). The external hypha was black in color, closely resembling that of known cultures of Cenococcum graniforme. Vegetative growth in MMN medium was very slow (1 cm in 1 month). This fungus was isolated from roots of seedlings receiving the SN and UI treatments.

Isolate 4 was obtained from morphological forms D and E (Table 37). The mycelium was lighter black than that of isolate 3. Clamp connections were not observed (Figure 27). Mycelial characteristics and slow growth in MMN medium suggest that this fungus is a strain of C. graniforme. This fungus was isolated from roots of seedlings receiving the PT and UI treatments.

Isolate 5 was derived only from the morphological form L. The color of the mycelium was white. Clamp connections (Figure 28) were occassionally seen but not as frequently as in isolates 1 or 2. Mycelium of this fungus closely resembled that of a fungus previously isolated from the basidiocarp of Laccaria laccata growing in the same area. This fungus was isolated from roots of seedlings receiving the SN and UI treatments.

Isolate 6 could not be identified by comparing the mycelium of this

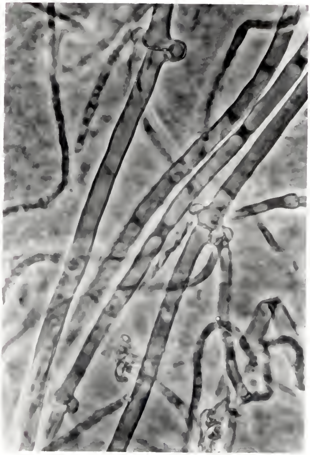

Figure 25. Microscopic characteristics of mycelia of isolate 2 showing clamp connections. (Identified as Pisolithus tinctorius). 1,200 X

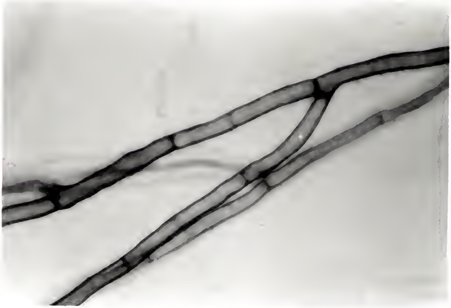

Figure 26. Microscopic characteristics of mycelia of isolate 3. (Identified as Cenococcum graniforme strain 1). 1,200 X

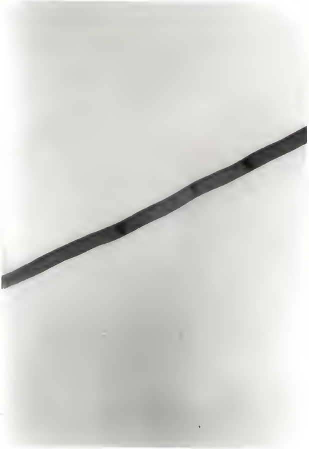

Figure 27. Microscopic characteristics of mycelia of isolate 4. (Identified as Cenococcum graniforme strain 2). 1,200 X.

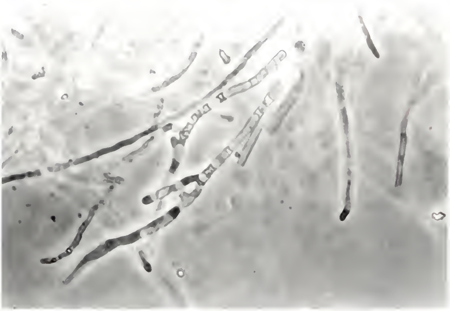

Figure 28. Microscopic characteristics of mycelia of isolate 5 with the presence of occassional clamp connections. (Identified as Laccaria laccata). 1,200 X.

fungus with that of known cultures of ectomycorrhizal fungi. This fungus was isolated from four morphological forms (Table 37). The mycelium was white with no evidence of clamp connections (Figure 29). This fungus was isolated from roots receiving PT and SN treatments.

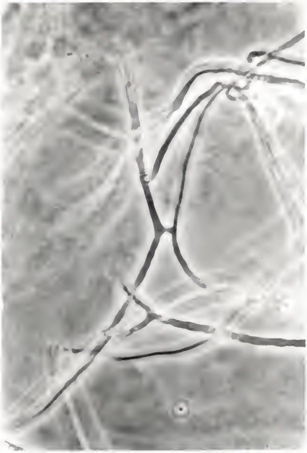

Figure 29. Microscopic characteristics of mycelia of isolate 6. (Unidentified). 1,200 X.

DISCUSSION

Ammonium nitrate was applied in a band to the surface of a Myakka soil at rates of 22 and 90 kg N/ha. Nitrogen concentration of the surface 15 cm was increased from 0.050 to 0.081% as a result of the addition of 90 kg N/ha (Table 2). Nitrogen concentration in the same soil was reduced to the original level of 0.050% after 10 months, indicating a rapid loss of N from the surface. Low cation exchange capacity of this soil (4.6 meq/100 g) and high rainfall (Ave. 11.39/month, Table 4) during the experimental period may have induced considerable leaching of applied N. The loss of N from the soil surface should be critically evaluated. Over an extended period of time, (5-10 years) slash pine seedlings may not continue the significant growth responses to N fertilization which were obtained in this study. This would necessitate additional appliation of N fertilizer to insure continued high productivity. The possibility of using slow-release N such as ureaformaldehyde or sulfur-coated urea, rather than soluble ammonium nitrate, should therefore be explored.

Phosphorus applied as concentrated superphosphate at rates of 22 and 90 kg P/ha was also lost from the soil surface (Table 2). Total and extractable P concentrations of the unamended soil were 61 and 2 ppm, respectively. After the addition of 90 kg P/ha, the total and extractable P concentrations were increased to 96 and 34.9 ppm, respectively. Moreover, total and extractable P were not reduced to the initial soil concentrations, 10 months after fertilization. This implies that the Myakka soil had some capacity to retain P. Organic matter content of this soil (2.83%) may account for some of the P retained. In addition, the acidic reaction (pH 4.5 in H_2O) of the soil may have increased the phosphate-binding activity of Al and Fe.

Considerable movement of N and P from the surface soil occurred because accumulations in the spodic horizon were detected (Table 3). The spodic horizon was located at an average depth of 55 cm below the surface. This is significant because the roots of slash pine will reach this horizon after 2-3 years or earlier. The roots, with their associated mycorrhizal fungi, might then tap this accumulated N and P. Over a period of time, the spodic horizon may be beneficial because of this accumulating capacity.

No significant difference was observed among mycorrhizal treatments in the survival of seedlings in the field (Table 6). This is probably a result of the high amount of precipitation (Table 4) which fell over the area after the seedlings were planted.

Growth responses of seedlings receiving four initial mycorrhizal treatments were statistically significant after 10 months of growth in the field (Tables 8, 10, 13, 14, 17, 18, 19, 21, 24, 25, 26, 27, 28, 30, and 32). The SN treatment caused significantly higher growth responses in slash pine seedlings than did the TT, PT, and UI treatments. The high positive responses from the SN treatment were probably due to (1) better preadjustments of seedlings to field conditions during the nursery phase of growth, (2) the presence of several indigenous ectomycorrhizal fungi in the roots, (3) ideal nutrient concentrations in the tissues brought about by standard fertilizer applications in the nursery, and (4) difference in age of seedlings when outplanted.

Nursery-grown seedlings were 3 months older than those grown under controlled conditions and receiving TT, PT, and UI treatments.

Better preadjustments to field conditions by the SN treatment were attained from the geographical design of the experiment. The SN seedlings were grown in a nursery (Container Corporation Nursery) and outplanted in the field (Austin Cary Memorial Forest) both of which were located in north-central Florida. The TT, PT, and UI treatments were raised in a growth room (PT and UI) or in a greenhouse (TT) in Athens, Georgia, but were outplanted in the same field as the SN treatment. The Georgia-grown seedlings were, therefore, completely isolated from actual field conditions before they were outplanted.

Thirty five percent of the feeder roots of seedlings receiving the SN treatment were mycorrhizal (Table 5). No attempt was made to isolate and identify the ectomycorrhizal fungi from these seedlings. The nursery, however, was surrounded by slash pine plantations, which should contain several ectomycorrhizal fungi. The nursery had also been planted repeatedly with generations of slash pine. Basidiospores and vegetative mycelia of different ectomycorrhizal fungi were apparently present in the soil to serve as effective source of inocula for root colonization. Populations of fungi may be reduced by fumigation during nursery establishment, but viable inocula persisted or were introduced in sufficient quantity as basidiospores to induce root colonization.

High growth responses by the SN treatment may also be attributed to the nutrient concentrations in the root and shoot tissues of seedlings prior to outplanting. This is shown in Table 5, particularly for the nutrients K, Ca, Mg, Al, Cu, Mn, Na, Fe, and Zn. The nutrient concentrations of the SN treatments were usually lower than those of the TT, PT, and UI treatments. Since the seedlings grown in the nursery exhibited larger growth than the Georgia-grown seedlings the low nutrient concentrations may be attributed to dilution effect.

Growth responses in the TT treatment were significantly larger than those treated with PT. Since similar growth conditions were imposed on these two mycorrhizal treatments, _T. terrestris_ is the ectomycorrhizal fungus ecologically adapted to the acidic, poorly-drained Myakka sands of Florida, and possibly other related soils. Basidiospores of _T. terrestris_ introduced into soil, have been shown to form ectomycorrhizae with pine seedlings (Marx and Ross, 1970). This is a significant point because _T. terrestris_ produces abundant basidiospores which may serve as a cheap and readily available source of inocula.

Growth responses by the UI seedlings were significantly less than those of the seedlings receiving the SN, TT, and PT treatments. This demonstrates the importance of mycorrhizal roots. The SN, TT, and PT treatments, which possessed mycorrhizal roots during the time of outplanting, had an initial advantage over the UI treatment in their greater capacity to absorb nutrients from the soil. The UI seedlings were later colonized by indigenous ectomycorrhizal fungi, but by then the growth of seedlings receiving the SN, TT, and PT treatments was more advanced.

Nitrogen is an essential constituent of amino acids, proteins, purines, chlorophyll, and many vitamins (Kramer and Kozlowski, 1960). In this present study, all growth responses increased significantly as the N fertilizer rates increased (Tables 9 and 22). The positive growth responses to increasing N rates emphasize the importance of N fertilization.

Regression equations between growth responses and N rates were linear (Table 9 and 22), except for the number of stem flushes. The linear responses may be attributed to the amount of N absorbed by seedlings at different N rates. When N fertilizer was not applied, the roots absorbed only the available N from the soil. With the addition of 22 kg N/ha, available N was increased, resulting in increased absorption by the plant roots. At the 90 kg N/ha, the pool of available N was larger than that at the 0 or 22 kg N/ha, therefore, more N was absorbed. The N was assimilated by the pine seedlings in relation to the amount of N absorbed. The difference in the assimilation of N at varying N rates was ultimately expressed as linear growth responses. The linearity of responses to N rates, however, may not be maintained after some time, because of the rapid removal of N from the root zone.

Number of stem flushes showed a quadratic response to N rates (Table 9). This response is difficult to explain because stem flushing may also be influenced by environmental factors such as temperature and photoperiod (Zimmerman and Brown, 1971). Number of stem flushes was significantly less at the unfertilized treatments than at those fertilized with 22 and 90 kg N/ha, suggesting that N application played a role in stem flushing. The exact role of N was not studied, but protein concentrations or hormonal balance may be suspected (Zimmerman and Brown, 1971). No significant difference in the number of stem flushes was observed between 22 and 90 kg N/ha, implying that the N requirement for stem flushing was met at 22 kg N/ha. Since more N was absorbed at 90 kg N/ha, the extra N not utilized for stem flushing may have been used in other growth processes such as height, root growth, and biomass production.

Mycorrhizae-nitrogen interaction was observed in the responses number and length of secondary branches (Tables 15 and 16, respectively). At 0 and 22 kg N/ha, the UI treatment showed significantly fewer and shorter secondary branches than did the SN, TT, and PT treatments. At 90 kg N/ha, the number and length of secondary branches were significantly larger in the TT and PT treatments than in the SN and UI treatments. Mycorrhizal treatments, particularly TT and PT, promoted the number and length of secondary branches. The exact cause of these responses is difficult to explain. Secondary branch development, however, is usually influenced by growth hormones (Zimmerman and Brown, 1971). Ectomycorrhizal fungi produce growth hormones, particularly IAA, in pure culture (Slankis, 1971). It is not known whether this fungus-produced auxin is translocated from the roots upwards into the branch primordia where it could augment the activity of plant-produced auxin.

Formation of more and longer secondary branches in pine seedlings, brought about by N fertilization, is a significant observation. Secondary branches usually promote more needle fascicles, thereby increasing the effective photosynthetic area. Nitrogen fertilization of Douglas-fir has been shown to increase the number and size of needles (Brix and Ebell, 1969) and to increase the rate of photosynthesis in detached 1-year old shoots (Brix, 1971).

Phosphorus is required in large amounts because of its role as a constituent of nucleoproteins, phospholipid, and ATP, the main medium for energy transfer in plants (Kramer and Kozlowski, 1960). In this present study, responses to P fertilization were significant for all growth parameters measured (Table 9 and 22), except for the number of secondary roots. The positive growth responses to P fertilization are important under Florida conditions, where the native P content and retention capacity of most soils are usually low.

Growth responses to all P fertilizer rates were quadratic (Tables 9 and 22), except for oven-dry weight of shoots which gave a linear response. Responses increased with the application of 22 kg P/ha but tended to level off at 90 kg P/ha. This consistent curvilinear response to P rates may be explained from the soil chemical analyses. Extractable or plant available P was still evident in the surface, 10 months after the application of 90 kg P/ha. (Table 2). The Myakka soil may retain some of the P in the exchange complex. Factors contributing to P retention could be the organic matter content of the soil (2.83%) and low soil pH (4.5 in H_2O), which would increase the phosphate-binding activity of Al, Fe, and probably Mn. If the P is held by Al, Fe, or Mn, this may later be recovered by pine roots, with the aid of the associated ectomycorrhizal fungi. Mycorrhizal fungi have been shown to increase the absorption of P from unsoluble P sources such as apatite (Stone, 1949).

Mycorrhizal-phosphorus interactions were observed in the growth responses fresh and oven-dry weight of shoots and for total fresh and dry biomass production (Tables 11 and 12). All these parameters refer to weight of seedlings *per se*. When P fertilizer was not applied, the SN and TT mycorrhizal treatments gave significantly higher weight responses than did the PT or UI treatments. By increasing the P rates to 90 kg P/ha, significant differences in weight were observed among the SN, TT, PT, and UI treatments. The weight responses can be attributed to the differential efficiency of P absorption by the various mycorrhizal treatments. The SN treatment was most efficient in absorbing P followed (in decreasing order of efficiency) by the TT, PT, and UI treatments. The significant increase in biomass production resulting from mycorrhizal-phosphorus treatment is obviously important in pine plantation establishment.

Ectomycorrhizal root formation increased with application of 90 kg N and P/ha as compared to that in unfertilized treatments (Table 22). This may appear in conflict with common observation of decrease mycorrhizal formation as the soil fertility level increases (Harley, 1969). However, evidence had been presented that the applied N and P had been leached away from the root zone (Table 2). The increased formation of mycorrhizal roots at 90 kg N and P/ha was therefore a reflection of the low soil fertility after 10 months.

Nitrogen concentrations in root and shoot tissues generally increased with increasing rates of N fertilizers (Table 33). Concentrations in the shoot tissues were higher than in the root tissues, indicating that N was readily translocated to shoots after absorption. Concentrations in root and shoot tissues of the PT and UI treatments were higher than those in the SN and TT treatments. Since growth was larger in the SN and TT treatments, the low N concentrations can be attributed to dilution effects.

Phosphorus concentrations in root and shoot tissues increased as the rates of applied P were increased (Table 35). Phosphorus concentrations of seedlings which did not receive P fertilizers were in the critical P range of 0.09-0.10% reported by Pritchett (1967) for 5-8 year old slash pine seedlings in flatwood sites. Critical level was defined as the concentration at which trees with a higher concentration of needle P would not be expected to respond to P fertilizations, while those trees with a lower needle P concentration would normally respond (Pritchett, 1967). Concentrations of all seedlings which received P fertilizer were greater than the reported critical range which definitely indicated a positive response to P fertilization.

The concentrations of K, Ca, and Mg in root and shoot tissues of all mycorrhizal treatments (Appendices 1, 2, and 3, respectively) generally increased as the N-P fertilizer rates were increased. Since only N and P fertilizers were added, it can be presumed that the increased K, Ca, and Mg concentrations were caused by better growth of N-P fertilized trees. This is significant because of the function of these nutrients in plant metabolism. Potassium plays a critical role in the translocation of carbohydrates and in N metabolism (Kramer and Kozlowski, 1960). Calcium is an important structural constituent of the middle lamella and functions as a cofactor of some enzymes (Evans and Sorger, 1966). Magnesium is a component of chlorophyll and is required for the activity of several enzymes (Kramer and Kozlowski, 1960).

Concentrations of Al and Fe in root and shoot tissues of all mycorrhizal treatments (Appendices 7 and 8, respectively) usually increased as the N and P fertilizer rates were increased from 0 to 22 kg N and P/ha, but decreased at 90 kg N and P/ha. The decrease in Al and Fe concentrations at 90 kg N and P/ha were due to dilution effects, since growth of seedlings at these rates was significantly high. Aluminum is not usually considered as an essential nutrient, but the plant roots absorb large amounts of this element. An excess of Al in plant tissues is highly toxic (Kramer and Kozlowski, 1960). Iron functions in the synthesis of chloroplast non-heme proteins, and occurs in a number of respiratory enzymes such as peroxidases and cytochrome oxidases (Evans and Sorger, 1966; Kramer and Kozlowski, 1960). Aluminum and Fe concentrations are higher in root tissues than in shoot tissues, indicating that the two nutrients are relatively immobile in pine tissues.

The essential role of Na in plant nutrition is still controversial. Experiments attempting to establish its essentiality have usually been made with lower plants (Evans and Sorger, 1966). However, pine seedlings absorbed Na in large quantities. Work should be done in the future to study the fate of absorbed in Na in pines. Copper is an essential constituent of the enzymes ascorbic acid oxidase, tyrosinase, laccase, and cytochrome oxidase (Evans and Sorger, 1966; Kramer and Kozlowski, 1960). The concentrations of Na and Cu (Appendices 11 and 12, respectively) usually increased as the N-P fertilizer rates increased from 0 to 22 kg N or P/ha. However, Na and Cu concentrations in tissues generally decreased at 90 kg/ha of N and P, indicating a dilution effect. Root tissues contained more Na and Cu than did the shoot tissues indicating the immobile nature of these nutrients in pines.

The observed trends in Mn concentrations (Appendix 15) in the root and shoot tissues are hard to explain. Concentrations are usually high at 0 and 90 kg P/ha and low at 22 kg P/ha. A physiological explanation for this phenomenon has not been reported before. Manganese activates enzymes such as dehydrogenases, decarboxylases, kinases, peroxidases (Evans and Sorger, 1966) and is important in the synthesis of chlorophyll (Kramer and Kozlowski, 1960), so that high concentrations in shoots than roots is obviously desired. Manganese concentrations in these experiments were usually higher in the shoot tissues than in roots although Mn is relatively immobile in plants (Kramer and Kozlowski, 1960).

Zinc is involved in the synthesis of tryptophane, the precursor of IAA (Kramer and Kozlowski, 1960) and is an essential constituent of the enzymes dehydrogenases, phosphatases, and peptidases (Evans and Sorger, 1966). Zinc concentrations of root and shoot tissues (Appendix 16) usually increased as the N-P fertilizer rates were increased. The increased concentrations of Zn were probably due to improved absorption caused by better growth of seedlings receiving N-P fertilizers.

The accumulation of the 11 nutrients N, P, K, Ca, Mg, Al, Fe, Na, Cu, Mn, and Zn (Tables 34 and 36, Appendices 4, 5, 6, 9, 10, 13, 14, 17, 18, respectively) by root and shoot tissues followed the general trends observed for the different growth parameters. More nutrients were accumulated by seedlings receiving the SN mycorrhizal treatment, followed by those from the TT, PT, and UI treatments. This clearly shows that mycorrhizal treatments influenced the accumulation of nutrients. Mycorrhizae are known to aid in nutrient absorption (Bowen, 1973; Harley, 1969). The accumulation of the 11 nutrients by root and shoot tissues also increased as the N-P fertilizer rates were increased. This behavior is correlated with the improved growth resulting from N-P fertilization.

Roots accumulated more Al and Fe (Appendices 9 and 10, respectively) than the shoot tissues. Aluminum is known to be toxic at high concentrations especially if this occurs in the foliage (Kramer and Kozlowski, 1960). Slash pine grows well in the acidic soils of Florida where the activity of Al is usually high. Slash pine roots appear to tolerate high concentrations of Al; therefore, high Al accumulation in the root is no cause for concern as long as it is not translocated in large quantities to the shoot tissues. Upward translocation in large quantities of Al is not probable because Al is relatively immobile in plants (Kramer and Kozlowski, 1960). Accumulation of Fe was higher in the roots than in the shoot tissues. Since Fe is involved in the synthesis of chloroplast proteins and is relatively immobile in plants (Kramer and Kozlowski, 1960), greater accumulation of this nutrient in the root may create mild deficiency problems, especially if fertilized seedlings continue their significant growth responses.

The ectomycorrhizal fungus Thelephora terrestris was consistently reisolated from seedlings receiving the SN, TT, PT, or UI treatments. Pisolithus tinctorius was gradually succeeded by T. terrestris or Cenococcum graniforme. Pisolithus tinctorius is known to form more ectomycorrhizal roots than T. terrestris when the soil temperature is increased from 24 to 34°C (Marx et al., 1970). This high temperature condition does not occur in flatwood sites for long periods of time because of the cooling effect of a high water table. This may explain why P. tinctorius was gradually replaced by indigenous ectomycorrhizal fungi. The differential growth responses of seedlings inoculated with T. terrestris and P. tinctorius demonstrates the ecological-physiological significance of site-adapted fungal symbionts.

The uninoculated seedlings were colonized by T. terrestris, C. graniforme, Laccaria laccata, and an unidentified fungus. This shows that the Myakka soil contained indigenous populations of T. terrestris and other ectomycorrhizal fungi. The consistent isolation of T. terrestris from roots of seedlings receiving the UI treatment further proves that this fungus is ubiquitous in the Myakka soil. Cenococcum graniforme is believed to be ecologically adapted to dry soil conditions (Mikola, 1948; Worley and Hacskaylo, 1959); thus the consistent observation of *C. graniforme* in roots conflicts with these earlier reports. Some strains of *C. graniforme* are, therefore, adapted to the sandy, acidic, and poorly-drained Myakka soil.

Thelephora terrestris and *P. tinctorius* were isolated from several morphological forms of ectomycorrhizae (Table 37). It is difficult to differentiate the two fungi on the basis of mycorrhizal morphology alone. However, the distinctive yellow color of *P. tinctorius* aids in the identification of this fungus. *Thelephora terrestris* forms a white fungal mantle. This is not a reliable criterion for identification since other ectomycorrhizal fungi also form a white mantle (Trappe, 1962). The mycorrhizae formed by *C. graniforme* and *L. laccata* were easily identified by their characteristic morphological forms.

Additional descriptive work is needed in order to associate specific morphological forms of mycorrhizae with respective mycorrhizal fungus. Dominik's classification scheme (1959), which combined morphological and anatomical characteristics of mycorrhizal roots, is useful for differentiating between morphological forms. Histological and cytological studies, and fluorescent microscopy techniques as described by Zak (1971) should be studied further, as a possible means of identifying the fungi associated with different forms of mycorrhizae.

Current nursery practices include soil fumigation designed to control damping-off fungi, nematodes, and weeds. Methyl-bromide fumigation reduced populations of mycorrhizal fungi in soil (Filer and Toole, 1968). It is therefore important in future mycorrhizal studies to investigate the feasibility of inoculating *T. terrestris* directly into nursery beds and to compare the growth and survival of inoculated seedlings with standard nursery-grown seedlings in the field.

Assuming that inoculation with T. terrestris is feasible and that in the future,studies will prove inoculated seedlings to give better growth responses than standard nursery seedlings, especially in adverse sites, inoculation could be justified as a part of standard nursery practices. The incorporation of an inoculation program will not adversely alter current nursery practices, because the inoculum (basidiospores or vegetative mycelia) can be applied with the mulch or be broadcasted by hand after seed sowing.

Inoculation with specific ectomycorrhizal fungi may prove significant if seedlings are outplanted in adverse sites or in areas which have never been planted with pines. Strip-mining areas, in Florida and elsewhere, are reapidly expanding. These areas usually contain toxic levels of Al, Mn, Cu, and S. Reforestation of strip-mining areas in the North is already being attempted and inoculated seedlings appear to do well. The favorable growth responses of trees following mycorrhizal inoculations in afforestation work are well documented (Harley, 1969; Hatch, 1936; Mikola, 1970).

Several interesting observations were made during this study which merit further investigation. The observed accumulation of N and P, and the probable accumulation of other nutrients, in the spodic horizon needs to be investigated thoroughly. Studies can be aimed at the comparative availability of accumulated nutrients to slash pine roots, the efficiency of pine roots to utilize these accumulated nutrients, the nutrient-fixing mechanisms involved, and the effects of fluctuating water table on nutrient accumulation and availability.

Future mycorrhizal work should be directed to (1) determining the feasibility of inoculating specific mycorrhizal fungi directly into nursery beds, (2) studying different ectomycorrhizal fungi, or strains of an ectomycorrhizal fungus, in their performance under different environmental conditions, (3) expanding the experimental sites to include adverse areas like the sandhills or P-deficient sites of Florida, and (4) using other mycorrhizal hosts like sand and loblolly pines.

Finally, three seedlings receiving each mycorrhizal-fertilizer treatments are still growing in the field. Growth responses, survival, and mycorrhizal succession data should be obtained from these seedlings after 5 or 10 years. Reapplications of N-P fertilizers may also be carried out.

SUMMARY AND CONCLUSIONS

Slash pine seedlings received TT, PT, UI, or SN mycorrhizal treatments. The seedlings were outplanted in the field. Four months after outplanting, nine N-P fertilizer rates were superimposed upon the mycorrhizal treatments in a split-plot design. The fertilizer rates consisted of factorial combinations of 0, 22, and 90 kg N and P/ha. Ammonium nitrate and concentrated superphosphate were the sources of N and P, respectively. The seedlings were harvested 10 months after fertilization. Various root and shoot growth parameters were measured. Tissue analyses determined the concentrations and accumulations of N, P, K, Ca, Mg, Al, Fe, Na, Cu, Mn, and Zn. Ectomycorrhizal roots were classified according to morphological forms to help identify the fungal symbiont. Reisolation experiments were conducted to determine if T. terrestris and P. tinctorius continued to colonize the inoculated roots or if they were replaced by other indigenous species of ectomycorrhizal fungi.

It is concluded that:

1. Mycorrhizal treatments gave significant responses in height, fresh and oven-dry weights of roots and shoots, number of secondary branches, length of the longest secondary branch and root, stem diameter, frequency of stem flushes, length of primary root, mycorrhizal root development, and total fresh and dry biomass production. The magnitude of the growth responses was in the order of SN $\geq$ TT $\geq$ PT $\geq$ UI treatments.

2. All growth parameters responded significantly to N rates. Growth responses were linear except for the frequency of stem flushes which responded quadratically to N rates. Response to N rates was in the order of: 90 $\geq$ 22 $\geq$ 0 kg N/ha.

3. Growth responses of seedlings were significantly increased by P fertilization except for the number of secondary roots. Responses to P rates were quadratic except for the oven-dry weight of roots. Phosphorus rates affected the growth responses of seedlings in the order of: 90 = 22 $\geq$ 0 kg P/ha.

4. Interactions between mycorrhizal treatments and N rates occurred in the number and length of secondary branches. The TT and PT mycorrhizal treatments together with 90 kg N/ha gave the highest number and length of secondary branches.

5. Mycorrhizal treatments interacted with P rates to yield significant responses in fresh and oven-dry weight of shoots and total fresh and dry biomass production. The SN and TT mycorrhizal treatments in combination with 90 kg P/ha stimulated significantly larger responses in these weight parameters.

6. Mycorrhizal treatments and N-P fertilization increased the accumulation by root and shoot tissues of N, P, K, Ca, Mg, Al, Fe, Na, Mn, Cu, and Zn.

7. *Thelephora terrestris* is maintained in the pine roots after 15 months of growth in the field. *Pisolithus tinctorius* was replaced gradually by *T. terrestris* and other ectomycorrhizal fungi. *Thelephora terrestris* is the ectomycorrhizal fungus best ecologically adapted to the sandy, acidic and poorly-drained Myakka soil of Florida, and probably other related soils.

8. Morphological forms can aid in identifying mycorrhizal fungi. Cenococcum graniforme and Laccaria laccata may be identified using this technique.

9. Nitrogen and P were rapidly lost from the surface 15 cm of the Myakka soil. Phosphorus is weakly retained in the surface. Both N and P accumulated in the spodic horizon.

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APPENDIX

1. Potassium concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	%							
N_0P_0	.17	.26	.27	.40	.33	.40	.28	.43
N_0P_1	.29	.32	.43	.39	.50	.48	.42	.38
N_0P_2	.45	.47	.29	.35	.26	.34	.41	.43
N_1P_0	.29	.32	.37	.44	.32	.46	.23	.30
N_1P_1	.28	.38	.37	.50	.24	.33	.43	.47
N_1P_2	.47	.51	.52	.45	.46	.44	.36	.40
N_2P_0	.40	.35	.38	.39	.26	.27	.42	.42
N_2P_1	.37	.31	.36	.37	.41	.52	.44	.40
N_2P_2	.45	.48	.51	.47	.31	.35	.37	.42
Average	.35	.38	.39	.42	.34	.40	.37	.41

2. Calcium concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	%							
N_0P_0	.10	.20	.18	.30	.26	.24	.21	.23
N_0P_1	.15	.31	.24	.44	.22	.30	.22	.34
N_0P_2	.19	.48	.21	.29	.25	.35	.23	.36
N_1P_0	.23	.29	.20	.37	.19	.28	.18	.29
N_1P_1	.21	.29	.22	.33	.25	.35	.22	.30
N_1P_2	.19	.42	.24	.42	.21	.44	.24	.39
N_2P_0	.15	.31	.14	.30	.18	.22	.17	.30
N_2P_1	.14	.31	.19	.40	.17	.39	.20	.33
N_2P_2	.16	.43	.17	.40	.22	.36	.21	.39
Average	.17	.34	.20	.36	.22	.33	.21	.33

3. Magnesium concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	%							
N_0P_0	.044	.069	.067	.100	.096	.098	.081	.070
N_0P_1	.082	.097	.116	.108	.118	.109	.113	.108
N_0P_2	.102	.167	.102	.106	.093	.112	.105	.078
N_1P_0	.110	.104	.109	.113	.102	.110	.079	.092
N_1P_1	.105	.105	.123	.115	.104	.120	.114	.122
N_1P_2	.116	.133	.131	.126	.126	.139	.107	.117
N_2P_0	.088	.110	.092	.129	.086	.095	.087	.104
N_2P_1	.094	.111	.097	.126	.100	.121	.080	.131
N_2P_2	.094	.125	.097	.137	.114	.124	.103	.109
Average	.093	.113	.104	.118	.104	.114	.097	.103

4. Total K accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	--------------------mg K/root or shoot--------------------							
N_0P_0	4.5	24.2	13.8	20.6	2.0	7.9	15.2	114.4
N_0P_1	16.0	69.8	29.7	66.1	19.0	61.5	48.3	145.3
N_0P_2	50.9	152.1	15.3	64.1	3.9	17.9	54.9	198.8
N_1P_0	11.9	50.0	21.7	81.0	5.4	25.0	18.6	63.6
N_1P_1	19.6	87.0	22.0	110.2	7.6	35.6	58.5	210.0
N_1P_2	72.4	215.2	51.5	112.5	32.0	79.8	58.5	200.9
N_2P_0	50.0	106.0	36.0	76.4	13.0	33.2	40.3	112.2
N_2P_1	50.3	101.2	48.2	115.1	25.6	80.1	62.9	160.4
N_2P_2	83.1	241.9	61.3	124.0	15.5	50.8	77.0	258.3
Average	39.9	110.4	33.3	85.6	13.8	43.5	48.2	162.7

5. Total Ca accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	--------------------mg Ca/root or shoot--------------------							
N_0P_0	2.6	18.7	9.0	15.4	1.6	4.9	11.4	61.2
N_0P_1	8.3	67.7	16.6	73.9	8.4	38.7	25.1	127.6
N_0P_2	21.7	156.5	10.9	54.3	3.8	18.4	31.1	163.4
N_1P_0	9.4	45.3	11.6	67.5	3.2	15.1	14.6	61.5
N_1P_1	14.9	65.8	13.0	71.5	8.0	38.2	30.1	136.5
N_1P_2	29.1	177.2	23.8	105.0	14.7	78.6	61.2	192.6
N_2P_0	18.9	92.0	13.2	58.8	9.0	27.5	16.3	78.6
N_2P_1	19.0	100.1	25.5	124.4	10.7	60.1	28.8	132.3
N_2P_2	29.8	218.4	20.6	103.9	11.0	52.2	43.7	241.8
Average	17.1	104.6	16.0	75.0	7.8	37.1	29.1	132.8

6. Total Mg accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	------mg Mg/root or shoot------							
N_0P_0	1.15	6.33	3.43	5.20	.58	1.96	4.44	18.56
N_0P_1	4.53	20.96	7.98	18.08	4.48	14.08	12.86	41.01
N_0P_2	11.67	54.42	5.30	19.60	1.39	5.80	14.22	34.88
N_1P_0	4.52	16.35	6.29	20.72	1.73	5.95	6.40	19.42
N_1P_1	7.48	23.77	7.24	25.12	3.32	13.12	15.68	55.01
N_1P_2	17.73	55.92	12.95	31.44	8.85	25.00	17.20	58.13
N_2P_0	11.03	32.96	8.67	25.28	4.28	11.66	8.38	27.61
N_2P_1	12.80	35.89	13.00	39.14	6.31	18.65	11.52	52.70
N_2P_2	17.51	63.07	11.74	35.94	5.68	17.97	21.34	67.75
Average	9.83	34.41	8.51	24.50	4.07	12.69	12.45	41.67

7. Aluminum concentrations of root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	ppm							
N_0P_0	1814	304	2561	384	2424	283	1930	362
N_0P_1	3404	429	3255	425	2590	454	2139	395
N_0P_2	2015	475	4627	362	2726	412	1707	425
N_1P_2	2014	308	1930	333	2747	425	2023	241
N_1P_1	2980	354	2819	375	2169	262	1649	308
N_1P_2	2481	478	2959	441	2752	521	2270	318
N_2P_0	2517	320	3354	379	2480	299	1871	404
N_2P_1	2840	400	2344	473	2653	433	2659	386
N_2P_2	1426	524	1833	540	2541	449	1645	420
Average	2388	399	2854	412	2565	393	1988	362

8. Iron concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	ppm							
N_0P_0	1286	80	1517	71	5575	194	1264	73
N_0P_1	1565	99	1203	226	1336	94	851	165
N_0P_2	2148	79	2600	190	3195	117	779	69
N_1P_0	1035	57	1597	63	1938	88	1331	114
N_1P_1	1981	64	2070	74	1566	75	1184	48
N_1P_2	1107	61	1970	63	1245	68	1304	48
N_2P_0	1054	44	1648	78	1233	91	1526	80
N_2P_1	1305	134	874	60	945	75	1536	84
N_2P_2	704	91	734	63	1679	66	1030	54
Average	1354	75	1579	99	2079	96	1201	82

9. Total Al accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	--------------------mg Al/root or shoot--------------------							
N_0P_0	4.72	2.79	13.06	2.0	1.45	0.57	10.61	9.63
N_0P_1	18.72	9.26	22.46	7.13	9.84	5.86	24.38	14.98
N_0P_2	22.97	15.47	24.06	6.70	4.09	2.14	23.04	19.46
N_1P_0	8.26	4.87	11.19	6.13	4.67	2.29	16.38	5.12
N_1P_1	21.16	8,03	16.63	8.21	6.94	2.86	22.58	13.87
N_1P_2	37.96	20.19	29.30	11.02	19.27	9.37	36.55	15.81
N_2P_0	31.71	9.61	31.52	7.42	12.40	3.68	17.96	10.69
N_2P_1	38.62	12.91	31.41	14.71	16.71	6.67	38.29	15.49
N_2P_2	26.52	26.40	22.17	14.15	12.70	6.51	34.22	26.06
Average	23.40	12.17	22.42	8.61	9.79	4.44	24.89	14.57

10. Total Fe accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	--------------------mg Fe/root or shoot--------------------							
N_0P_0	3.34	0.74	7.73	0.37	3.34	0.39	6.96	1.94
N_0P_1	8.60	2.13	8.30	3.80	5.08	1.21	9.70	6.24
N_0P_2	24.49	2.58	13.52	3.52	4.79	0.61	10.52	3.17
N_1P_0	4.24	0.91	9.26	1.17	3.29	0.47	10.78	2.42
N_1P_1	14.07	1.45	12.22	1.62	5.01	0.82	16.22	2.18
N_1P_2	16.94	2.57	19.50	1.57	8.71	1.23	20.99	2.38
N_2P_0	13.28	1.31	15.49	1.52	6.16	1.12	14.65	2.12
N_2P_1	17.75	4.34	11.71	1.87	5.96	1.15	22.12	3.38
N_2P_2	13.10	4.56	8.88	1.65	8.39	0.96	21.43	3.34
Average	12.87	2.29	11.85	1.90	5.64	0.88	14.82	3.02

11. Sodium concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	ppm							
N_0P_0	1340	944	1214	782	1375	854	965	733
N_0P_1	1873	933	1381	783	1166	575	1149	579
N_0P_2	916	587	1232	853	1727	1066	1082	733
N_1P_0	1340	808	1506	1007	1297	1220	1515	1003
N_1P_1	1415	804	1297	733	1321	829	1157	920
N_1P_2	1246	836	1205	753	1289	858	1280	634
N_2P_0	987	674	1013	720	1224	703	956	691
N_2P_1	1203	794	1707	897	1239	841	1454	1039
N_2P_2	1344	927	1228	835	1799	981	1679	994
Average	1296	812	1309	818	1382	881	1249	814

12. Copper concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	ppm							
N_0P_0	5.00	3.77	5.00	4.17	5.23	3.37	4.20	4.17
N_0P_1	5.83	3.77	8.33	5.00	8.33	3.77	6.67	3.77
N_0P_2	8.40	4.20	7.50	3.77	9.20	2.50	7.50	6.67
N_1P_0	5.00	3.80	4.17	3.77	7.23	2.10	5.00	2.93
N_1P_1	7.50	5.00	8.33	4.60	5.43	2.77	6.67	5.83
N_1P_2	9.13	4.57	9.97	5.83	6.67	4.60	5.83	4.87
N_2P_0	5.00	4.60	5.00	5.00	7.07	3.37	5.83	6.20
N_2P_1	8.33	5.00	14.10	5.83	10.00	7.07	10.00	5.40
N_2P_2	7.50	5.83	10.77	6.20	9.97	3.37	6.67	4.57
Average	6.85	4.50	8.13	4.91	7.68	3.70	6.49	4.93

13. Total Na accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	-------------------mg Na/root or shoot--------------------							
N_0P_0	3.48	8.68	6.19	4.07	0.82	1.71	5.31	19.49
N_0P_1	10.30	20.15	9.53	13.15	4.43	7.41	13.09	21.93
N_0P_2	10.44	19.14	6.40	15.79	2.59	5.54	14.61	33.58
N_1P_0	5.50	12.76	8.73	18.53	2.21	6.59	12.27	21.27
N_1N_1	10.05	18.24	7.66	16.05	4.23	9.03	15.85	41.42
N_1P_2	19.06	35.29	11.93	18.82	9.02	15.44	20.61	32.54
N_2P_0	12.44	20.22	9.53	14.11	6.12	8.64	9.18	18.30
N_2P_1	16.36	25.64	22.88	27.89	7.81	12.95	20.94	41.67
N_2P_2	24.99	46.72	14.86	21.89	9.00	14.23	34.92	61.64
Average	12.51	22.98	10.86	16.70	5.14	9.06	16.31	32.43

14. Total Cu accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	----------mg Cu/root or shoot----------							
N_0P_0	.013	.035	.026	.022	.003	.007	.023	.111
N_0P_1	.032	.081	.058	.084	.032	.048	.076	.143
N_0P_2	.096	.137	.039	.070	.014	.013	.101	.305
N_1P_0	.021	.060	.024	.069	.012	.011	.041	.062
N_1P_1	.053	.114	.049	.101	.017	.030	.091	.263
N_1P_2	.140	.193	.099	.146	.047	.083	.094	.242
N_2P_0	.063	.138	.047	.098	.035	.041	.056	.164
N_2P_1	.113	.162	.189	.181	.063	.109	.144	.217
N_2P_2	.140	.294	.130	.162	.050	.054	.139	.283
Average	.074	.135	.074	.104	.030	.044	.085	.199

15. Manganese concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	ppm							
N_0P_0	42.4	268.0	45.7	283.2	71.4	209.9	40.8	261.8
N_0P_1	24.2	120.4	40.8	323.9	37.5	360.3	34.1	206.5
N_0P_2	34.2	244.8	33.3	209.0	51.0	288.2	36.5	221.7
N_1P_0	50.8	179.5	32.1	177.3	39.1	206.8	29.1	94.90
N_1P_1	33.8	157.0	51.0	244.4	36.2	127.0	29.1	138.7
N_1P_2	37.1	282.0	50.4	371.3	47.9	334.8	30.8	201.4
N_2P_0	55.6	280.0	37.4	265.5	30.6	141.4	30.8	177.9
N_2P_1	25.7	160.7	22.4	154.0	42.4	178.5	21.6	125.0
N_2P_2	37.7	262.3	51.9	400.7	42.3	213.3	31.2	197.7
Average	37.9	217.8	40.6	269.9	44.2	228.9	31.6	180.6

16. Zinc concentrations of root and shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	ppm							
N_0P_0	33.83	45.43	41.57	44.23	42.73	29.23	38.60	50.20
N_0P_1	39.17	30.17	69.40	71.77	58.63	48.77	35.47	36.80
N_0P_2	41.47	51.37	44.77	36.80	59.87	42.90	43.47	48.93
N_1P_0	47.47	45.07	37.77	44.37	38.07	40.03	46.43	35.30
N_1P_1	38.97	32.30	33.27	46.07	37.73	40.50	32.67	37.10
N_1P_2	66.13	70.07	62.67	44.83	44.93	48.57	37.58	41.03
N_2P_0	38.33	45.63	36.90	46.77	47.33	36.03	36.93	50.33
N_2P_1	43.27	40.97	45.07	40.43	46.20	61.10	53.87	46.03
N_2P_2	56.87	61.57	64.07	78.71	70.53	40.57	46.83	34.90
Average	45.06	46.95	48.39	50.44	49.56	43.08	41.32	42.29

17. Total Mn accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	---mg Mn/root or shoot---							
N_0P_0	.110	2.47	.233	1.47	.043	.42	.224	6.96
N_0P_1	.133	2.60	.282	5.44	.143	4.65	.389	7.83
N_0P_2	.390	7.98	.173	3.87	.077	1.50	.493	10.16
N_1P_0	.209	2.84	.186	3.26	.066	1.12	.236	2.01
N_1P_1	.240	3.56	.301	5.35	.116	1.38	.399	6.24
N_1P_2	.567	11.90	.499	9.28	.336	6.03	.495	10.03
N_2P_0	.701	8.40	.351	5.20	.153	1.74	.296	4.71
N_2P_1	.350	5.19	.300	4.79	.267	2.75	.311	5.01
N_2P_2	.695	13.22	.628	10.50	.212	3.09	.650	12.26
Average	.377	6.46	.328	5.46	.157	2.52	.388	7.25

18. Total Zn accumulated by root or shoot tissues of field-grown slash pine seedlings receiving four initial mycorrhizal treatments and nine N-P fertilizer rates

Fertilizer rates	Mycorrhizal Treatments							
	TT		PT		UI		SN	
	Root	Shoot	Root	Shoot	Root	Shoot	Root	Shoot
	mg Zn/root or shoot							
N_0P_0	.088	.418	.212	.230	.026	.058	.212	1.335
N_0P_1	.215	.652	.479	1.206	.223	.629	.404	1.395
N_0P_2	.472	1.675	.233	.681	.090	.233	.587	2.241
N_1P_0	.195	.712	.219	.816	.065	.216	.376	0.748
N_1P_1	.277	.733	.196	1.009	.121	.441	.448	1.670
N_1P_2	1.010	2.957	.620	1.120	.315	.874	.605	2.043
N_2P_0	.483	1.369	.347	.917	.237	.443	.355	1.333
N_2P_1	.588	1.323	.604	1.257	.291	.941	.776	1.846
N_2P_2	1.056	3.103	.775	2.062	.353	.588	.974	2.164
Average	.488	1.438	.409	1.033	.191	.492	.526	1.642

BIOGRAPHICAL SKETCH

Reynaldo E. de la Cruz was born on December 31, 1944 at Zamboanga City, Philippine Islands. He obtained his Bachelor of Science in Forestry degree (Major in Forest Management) in June, 1965 at the University of the Philippines (U. P.) College of Forestry. From 1965 to 1969, he joined the faculty staff of the U. P. College of Forestry where he worked as an instructor of Botany, Dendrology, and Plant Physiology. In March 1969, he entered the Graduate School of the University of Florida. He obtained his Master of Science in Forestry degree from the School of Forest Resources and Conservation in 1971. He then worked for his Doctor of Philosophy degree in the area of tree nutrition in the same University; this he later obtained in June, 1974.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

David H. Hubbell

David H. Hubbell, Chairman
Associate Professor of Soils

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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Principal Plant Pathologist, USDA

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor or Philosophy.

June, 1974

Asst Dean, College of Agriculture

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